

THE POSTCRANIAL SKELETON OF NORTH AMERICAN MULTITUBERCULATES

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ABSTRACT. Multituberculates are an extinct order of nontherian mammals commonly represented by teeth in late Mesozoic and early Tertiary terrestrial deposits. They are generally regarded as the first major mammalian group to have been predominantly herbivorous. The dentition of multituberculates is well known, but studies of their skeletons have been limited by the rarity of associated remains. In this study we describe a postcranial skeleton of *Ptilodus kummae*, the most complete known for a North American multituberculate. In addition, we review other North American multituberculate postcranial materials in an effort to identify the major structural and functional characteristics of the group.

Despite their diversity in size and in dental specializations, multituberculates as far as known exhibit little variability in their postcranial skeleton. This conclusion is based on a comparison of the specimens of *Ptilodus* with material representing or referable to the following genera: *Catopsalis*, *Cimexomys*, *Cimolodon*, *Ectypodus*, *Eucosmodon*, *Meniscomes*, *Mesodma*, *Stygimys*, and *Taeniolabis*.

Multituberculates possess a number of unusual and even unique postcranial features. These include a scapulocoracoid with a reduced coracoid but without a supraspinous fossa, an enlarged prepollex, a dorsally emarginate acetabulum, a postobturator foramen within the ischiopubic symphysis, a large parafibula, a slender, ventrally directed lateral flange on the proximal end of the fibula, a deep excavation posteriorly beneath the proximal articular surface of the tibia, a specialized tarsal structure (particularly that of the astragalus and calcaneum), and thoracic centra with the anterior epiphysal surface recessed ventrally and bulbous dorsally.

Ptilodus and *Eucosmodon*, the only two genera for which articulated foot bones are known, possess distinctive tarsal adaptations for a range of pedal mobility (especially abduction) characteristic of arboreal mammals that descend trees headfirst. The

hallux is divergent, and the entocuneiform-metatarsal I joint permitted considerable hallucal abduction and adduction for prehension in a plane independent of the remaining digits. The long, robust tail of *Ptilodus* possessed musculoskeletal features that, in modern mammals, are present in prehensile-tailed forms. We conclude that at least some multituberculates were arboreal.

INTRODUCTION

Multituberculates are an extinct group of nontherian mammals that have been recovered from North America, Europe, and Asia, and whose known range in geologic history extends from the Late Jurassic to the Oligocene (or possibly from the Late Triassic, if the Haramiyidae are multituberculates [Hahn, 1973]). Although multituberculate teeth are common in Late Cretaceous and Paleocene local faunas of North America, jaws and especially skulls are rare. Postcranial bones are also relatively rare, and the postcranial structure of multituberculates is therefore not well understood.

Several partial skeletons and isolated postcranial bones of multituberculates have been described within the past century. In 1973 a well-preserved and nearly complete skeleton of *Ptilodus kummae* was discovered in the Paleocene Ravenscrag Formation of Saskatchewan, a discovery that provided the impetus for this study of the postcranial skeleton of North American multituberculates. Our description centers largely on the specimen of *P. kummae* because of its unusual completeness. We have also reviewed previously published specimens, as well as additional multituberculate elements (some of which are of uncertain generic or specific identity) in order to provide a comprehensive account and a basis for assessing postural, locomotor, and other adaptations.

PREVIOUS WORK ON MULTITUBERCULATE POSTCRANIAL SKELETONS

Multituberculate postcranial bones are at present known only from North Amer-

ica and Asia. A synopsis of published work is given below.

NORTH AMERICA

In 1909 Gidley reported the discovery of an incomplete skeleton associated with the skull and lower jaws of *Ptilodus montanus* from the middle Paleocene of Montana. Preserved were a nearly complete cervical vertebra and some fragmentary caudal vertebrae, and parts of a humerus, radius, ulna, femur, tibia, fibula, pelvis, metapodials, and an ungual phalanx. On the basis of this material, Simpson (1926) attempted a reconstruction of multituberculate locomotor and feeding habits, and Jerison (1973) provided estimates of the body length and weight of *Ptilodus* (which have been criticized by Radinsky [1975]).

A well-preserved specimen of the hind limbs and pelvis of an undetermined species of *Eucosmodon* was recovered from early Paleocene deposits in New Mexico and was referred to in several reports (Granger, *in* Broom, 1914; Granger, 1915; Simpson, 1928a). Simpson and Elftman (1928) reconstructed the hind limb and pelvic musculature and made inferences concerning the habits of *Eucosmodon*. Granger and Simpson (1929) added a detailed osteological description of the specimen. Simpson (1937a) briefly compared the postcranial osteology of *Ptilodus* and *Eucosmodon*.

The less complete skeletons and isolated bones of North American multituberculates that have been described are:

- 1) Cope (1882a): an astragalus and caudal vertebrae of *Taeniolabis taoensis*. The astragalus, redescribed and figured by Cope in 1884a, was later shown by Matthew (1937) to probably belong to a condylarth (it is, at least, undoubtedly therian). Cope (1884a: pl. XXIIIc, figs. 3 and 4; 1884b: fig. 4b,c) also described and figured a humerus and ulna of *T. taoensis*. The ulna exhibits an articulation of the condylar type possessed by multituberculates (Jenkins, 1973).

- Sloan (1981: 158), however, is of the opinion that the humeral fragments "are from some indeterminate placental mammal."
- 2) Cope (1882b): the distal extremity of a humerus of *Meniscoessus conquistus* (figured by Cope, 1884b: fig. 7g; 1888: fig. 9g).
 - 3) Marsh (1889): a scapulocoracoid, the type of *Camptomus amplus*, together with an interclavicle, astragalus, and calcaneum provisionally referred to the same taxon. Serious doubts have been raised about the association and identification of these specimens (Simpson, 1928a,b; McKenna, 1961). Although McKenna (1961) accepted the astragalus and calcaneum as being those of a multituberculate, he regarded the interclavicle as problematical and provisionally referred the scapulocoracoid, the type specimen, to the Marsupialia.
- Marsh (1889) also figured the distal end of a humerus of "*Dipriodon lunatus*," a left semilunar, probably of "*Dipriodon*" *robustus*, and the proximal end of a femur of "*Halodon sculptus*." All three species are now referred to *Meniscoessus robustus* (see Clemens, 1963). The humerus and femur are undoubtedly from a multituberculate; the semilunar does not resemble the bone tentatively identified as a semilunar of *Ptilodus kummae*.
- 4) Granger and Simpson (1929): several skeletal fragments of *Stygimys teilhardi* including fragments of both ulnae and femora, the right humerus and ilium, the left tibia, a phalanx, and thoracic, sacral, and caudal vertebrae.
 - 5) Simpson (1937b: 737): "Skull . . . with associated femur, ulna, and some other fragments" of *Ptilodus montanus*. The postcranial remains include left and right femora, a lumbar vertebra, a proximal fragment of a phalanx, and the distal end of a left humerus; no ulna is present. The femora are definitely those of a multituberculate, the phalangeal fragment is much too large to belong to the same individual, and the humeral fragment, as Deischl (1964) previously noted, belongs to a therian.
 - 6) McKenna (1961): two partial scapulocoracoids from the Upper Cretaceous Lance Formation of Wyoming, designated as "Lance Type 1" and "Lance Type 2." Clemens (1963) provisionally allocated the Lance Type 1 and Type 2 scapulocoracoids on the basis of size and frequency to *Mesodma formosa* and *Cimolodon nitidus*, respectively.
 - 7) Deischl (1964): Scapulocoracoids, humeri, ulnae, radii, pelves, femora, tibiae, calcanea, and astragali from the Upper Cretaceous Bug Creek Anthills locality, Hell Creek Formation, Montana; these bones were variously assigned, on the basis of size and frequency data, to *Mesodma thompsoni*, *Mesodma formosa*, *Cimexomys minor*, *Cimolodon nitidus*, *Stygimys kuszmauli*, and *Catopsalis joyneri*. Sloan and Van Valen (1965) reconstructed the skeleton of *Mesodma thompsoni*.
 - 8) Sahni (1972): calcaneum and fragmentary humerus and femur of ?*Mesodma primaeva* and calcaneum of *Meniscoessus major*.
 - 9) Jenkins (1973): a left ulna (unidentified) and a right humerus referred to ?*Catopsalis*, both from the Bug Creek Anthills locality.
 - 10) Jenkins and Weijs (1979): a composite reconstruction of an unidentified multituberculate scapulocoracoid from the Bug Creek Anthills locality.
 - 11) Krause and Baird (1979): left femoral fragment of an unidentified multituberculate from the Mount Laurel Formation, New Jersey.

ASIA

References to published work on Asiatic multituberculate postcranial material

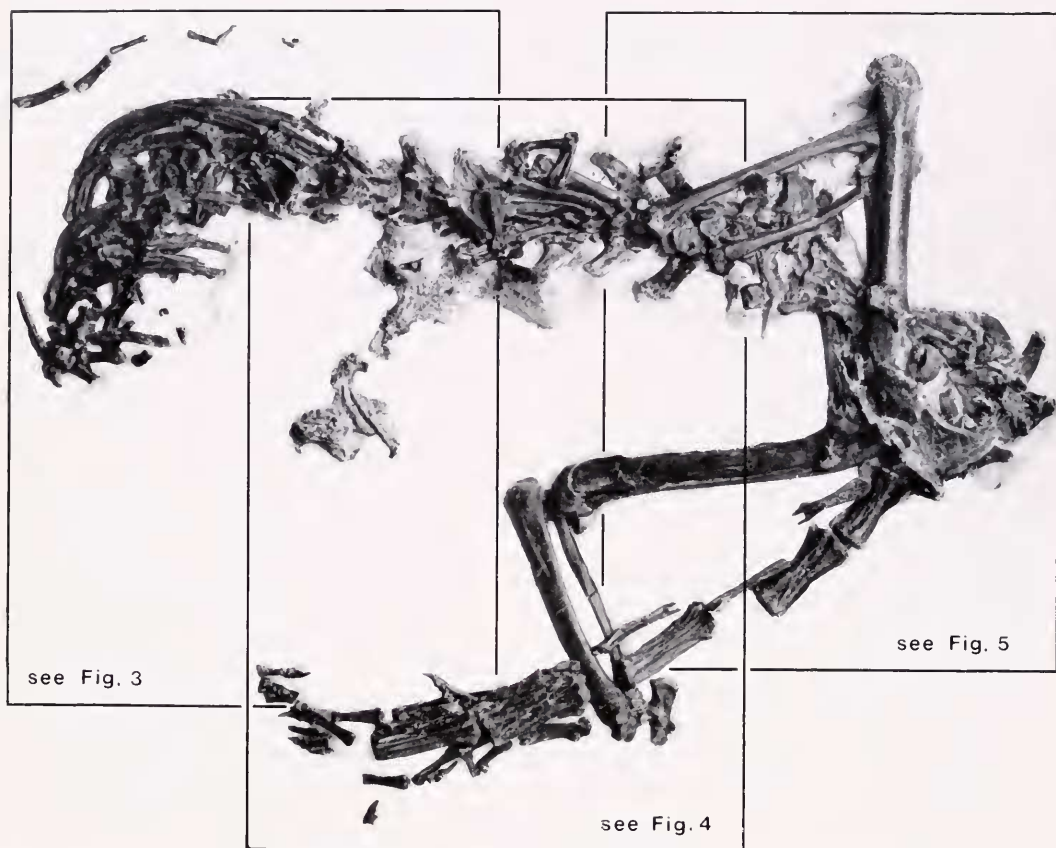


Figure 1. Left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). A key to stereophotographs of specific regions is shown. $\times 1.28$.

are included in this study because these materials offer additional and important insights.

Simpson (1928c: 9) described "several associated foot bones, five fragmentary vertebrae, the lower end of a scapula, a large part of a humerus, ribs and several other fragments" associated with the type skull of *Djadochtatherium matthewi* (AMNH 20440) from the Upper Cretaceous Djadokhta Formation of Mongolia. *Djadochtatherium* Simpson, 1925 is now considered to be a junior synonym of *Captopsalis* Cope, 1882c (Kielan-Jaworowska and Sloan, 1979). McKenna (1961) redescribed the fragmentary scapulocoracoid

in his review of the multituberculate shoulder girdle.

Recent discoveries by the Polish-Mongolian Palaeontological Expeditions to Mongolia include postcranial materials of at least four species of multituberculates from the Upper Cretaceous Djadokhta and Barun Goyot formations: a nearly complete skeleton of *Chulsanbaatar vulgaris* and partial skeletons of *Kryptobaatar dashzevegi*, *Nemegtbaatar gobiensis*, and *Sloanbaatar mirabilis* (Kielan-Jaworowska, 1970, 1974; Clemens and Kielan-Jaworowska, 1979). With the exception of accounts of the pelvis in *K. dashzevegi* (Kielan-Jaworowska, 1969, 1979) and the

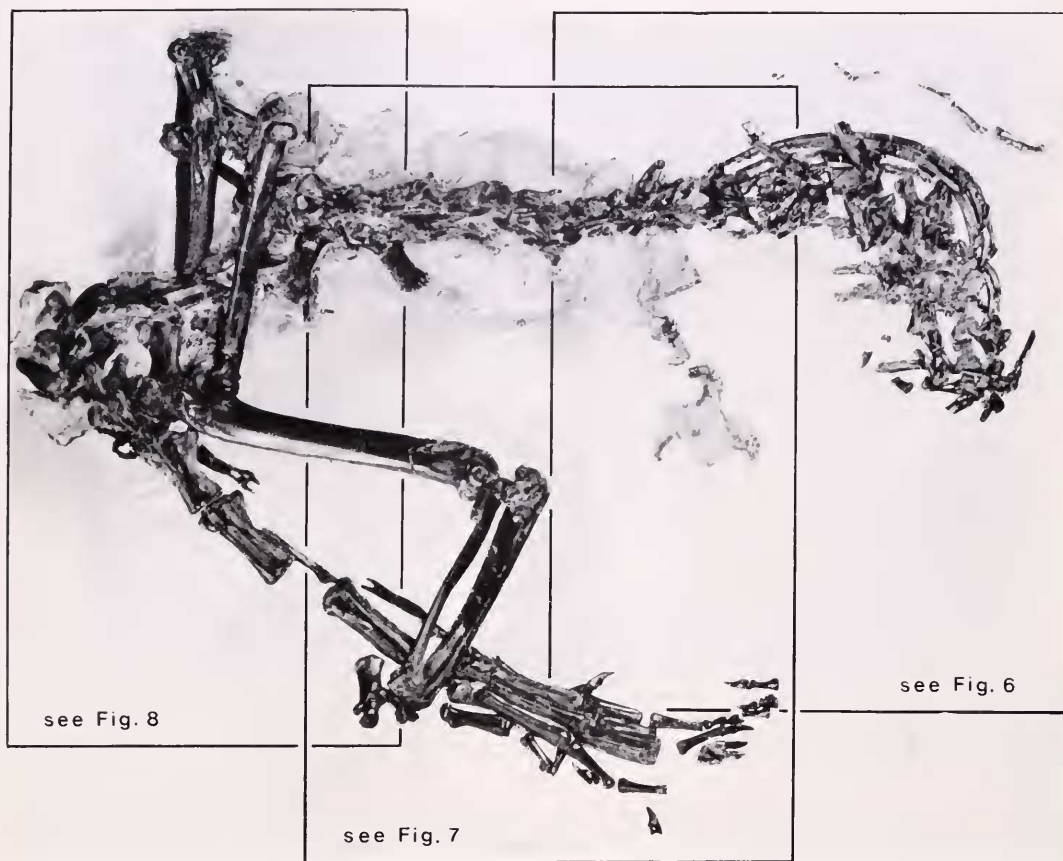


Figure 2. Right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). A key to stereophotographs of specific regions is shown. $\times 1.28$.

partial humeri and left ulna of *Tugrigbaatar saichanensis* from the Toogreeg beds (Kielan-Jaworowska and Dashzeveg, 1978), the material is as yet unpublished. However, Clemens and Kielan-Jaworowska (1979) provided some information on the Mongolian forms (studied by Kielan-Jaworowska) in their brief review of the multituberculate postcranial skeleton. The specimen of *T. saichanensis* is housed in the Institute of Geology of the Mongolian Academy of Sciences in Ulan Bator; all of the rest of this important Asiatic material is in the Institute of Paleobiology (Zakład Paleobiologii) of the Polish Academy of Sciences in Warsaw.

ABBREVIATIONS

Abbreviations used for the names of museums:

AMNH—American Museum of Natural History, New York

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

PU—Princeton University Museum, Princeton, New Jersey

UA—University of Alberta, Edmonton, Alberta

UCMP—Museum of Paleontology, University of California, Berkeley, California



Figure 3. Stereophotographs of anterior portion of left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). The area referenced to Figure 16 contains the ?right carpus. $\times 1.25$.

Abbreviations: Cd20, ?twentieth caudal vertebra; L1, presumed first lumbar vertebra.

UM—University of Michigan Museum of Paleontology, Ann Arbor, Michigan

UMVP—University of Minnesota, Minneapolis, Minnesota

USNM—United States National Museum, Washington, D.C.

YPM—Peabody Museum of Natural History, Yale University, New Haven, Connecticut

MATERIALS

TYPE SPECIMEN OF *PTILODUS KUMMAE* (UA 9001)

This specimen was discovered at a late Paleocene (Tiffanian) locality (UAR2g; see Krause, 1977) in the Ravenscrag Formation of Saskatchewan. Prior to discovery, the skull, both lower jaws, several anterior vertebrae, the pectoral girdle, most of the forelimbs, and some caudal vertebrae had eroded from the rock. Fragments of these

elements were recovered by surface collecting and by washing and screening the surrounding matrix. The fragments thus obtained include several teeth (left I_1 and P^1 ; right P_4 , M_1 , and P^{2-4}), the distal end of the right scapulocoracoid, fragments of the right humerus, proximal parts of both radii, a proximal segment of the right ulna, ten manual phalanges, and three caudal vertebrae. Association of these isolated elements with the articulated specimen is confidently established by the close proximity in which they were found, the virtual absence of bone in the immediately adjacent area, the anatomical correspondence to known allotherian skeletal elements (especially those of *Ptilodus montanus* described by Gidley [1909]), the absence of duplication of individual bones, and the close fit of some complex articular surfaces (for example, the humerus and ulna).

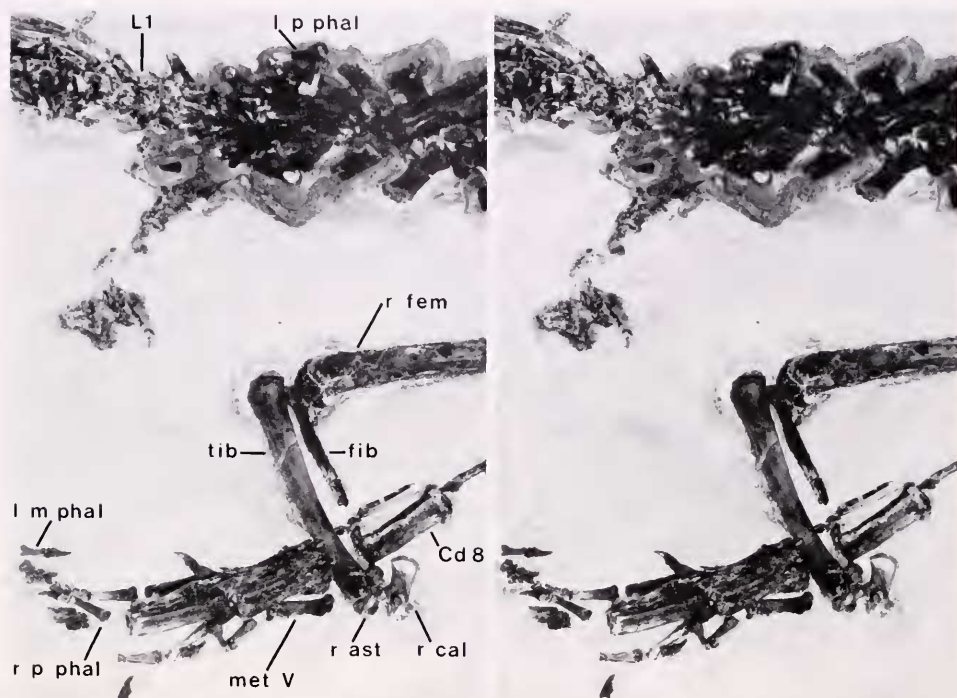


Figure 4. Stereophotographs of central portion of left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). For details of the right tarsal bones, see Figure 27B. $\times 1.25$.

Abbreviations: l, left; r, right; ast, astragalus; cal, calcaneum; Cd8, eighth caudal vertebra; fem, femur; fib, fibula; L1, presumed first lumbar vertebra; m phal, manual phalanges; met V, fifth metatarsal; p phal, pedal phalanges; tib, tibia.

The specimen as preserved *in situ* lay on its right side. This side was prepared first, and then covered with a white mold-making rubber (Silastic A RTV, Dow Corning Corp.). The specimen was then inverted and the left side prepared, a mold made, and finally embedded in clear Bioplastic (Ward's Natural Science Establishment, Inc.). This technique firmly secured the fragile, delicate bones and permits observation of both sides of the specimen. During preparation, the following bones were removed because they prevented exposure of critical areas of the skeleton: left calcaneum, left ectocuneiform, left metatarsal V, three phalanges of the left pes, a parafibula, and several smaller fragments, primarily pedal sesamoids.

The articulated portion of the skeleton

is virtually complete posterior to the anterior part of the rib cage (Figs. 1–8). The only portions of the pectoral limbs remaining intact are a poorly preserved distal segment of the ?right ?radius, most of the ?right carpus (with attached metacarpal and complete digit I, and the proximal portion of metacarpal II), and some middle and distal phalanges of the ?left manus. The long tail had curled around the anterior part of the body. A middle segment of the tail, containing approximately eight vertebrae, had weathered out prior to discovery.

OTHER MATERIAL

All known articulated postcranial remains as well as various disarticulated and

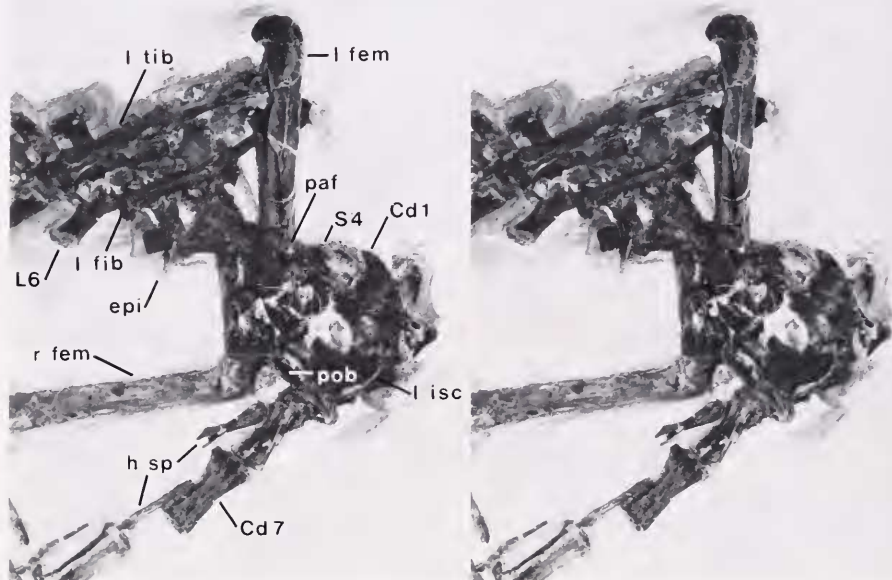


Figure 5. Stereophotographs of posterior portion of left side of postcranial skeleton of *Ptilodus kummae* (UA 9001). $\times 1.25$.

Abbreviations: l, left; r, right; Cd1, Cd7, first and seventh caudal vertebrae; epi, epipubic bone; fem, femur; fib, fibula; h sp, haemal spine; isc, ischium; L6, sixth lumbar vertebra; paf, parafibula; pob, postobturator foramen; S4, fourth sacral vertebra; tib, tibia.

fragmentary bones of North American multituberculates were studied. These were used primarily to describe features that are poorly preserved or missing in the specimen of *P. kummae* (UA 9001). This procedure, however, does not imply that the postcranial elements of different multituberculate taxa were identical in every detail; rather, it provides an outline of basic features, at least for ptilodontoids and taeniolabidoids. On present evidence, structural variability among ptilodontoid and taeniolabidoid postcranial bones is not so great as to diminish the utility of describing and making functional interpretations of a basic plan.

Definite generic and specific assignments of postcranial elements are possible only on the basis of associated dental material. Accordingly, we preface with a question mark all taxonomic allocations of isolated elements or partial skeletons that

lack dental remains. Materials of the following taxa, grouped according to locality, were available for this study:

- 1) Irvine locality, Late Cretaceous (Judithian), Judith River Formation, Alberta. Isolated elements (UA collections) not assigned to specific taxa.
- 2) Clambank Hollow locality, Late Cretaceous (Judithian), Judith River Formation, Montana. Isolated elements (AMNH collections) assigned by Sahni (1972) to ?*Mesodma primaeva* and *Meniscoessus major*.
- 3) Upper Hop Brook locality, Late Cretaceous, Mount Laurel Formation, New Jersey. Isolated femoral fragment (PU 21451) of an unidentified multituberculate (Krause and Baird, 1979).
- 4) Lull 2 Quarry (UCMP locality V-5620) and localities of uncertain location (Marsh, 1889; McKenna, 1961),

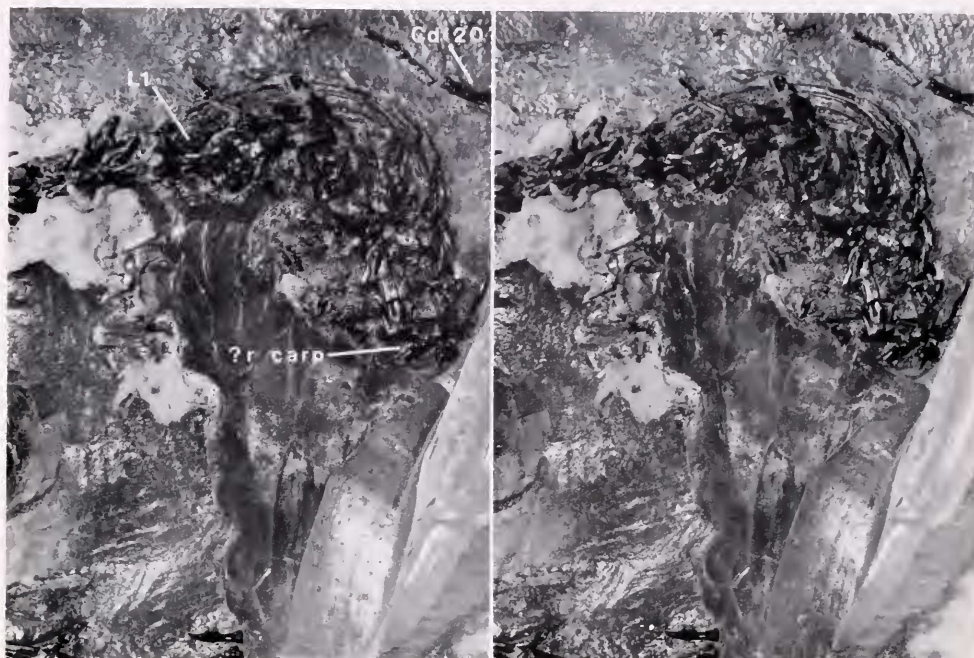


Figure 6. Stereophotographs of anterior portion of right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). $\times 1.25$. Abbreviations: ?r carp, ?right carpus; Cd20, ?twentieth caudal vertebra; L1, presumed first lumbar vertebra.

Late Cretaceous (Lancian), Lance Formation, Wyoming. Isolated elements in AMNH and YPM collections tentatively allocated to *Mesodma formosa*, *Cimolodon nitidus*, and *Meniscoessus robustus* (Clemens, 1963).

5) Type locality of *Meniscoessus conquistus*, Late Cretaceous (Lancian), "Laramie Formation," South Dakota. Humeral fragment (AMNH 3011a) of *Meniscoessus conquistus* (Cope, 1882b).

6) Bug Creek Anthills locality, Late Cretaceous (Lancian), Hell Creek Formation, Montana. Many isolated elements in AMNH, MCZ, UA, UCMP, and UMVP collections. The UMVP collections include bones referred to *Mesodma thompsoni*, *Mesodma formosa*, *Cimexomys minor*, *Cimolodon nitidus*, *Stygimys kuszmauli*, and *Catopsalis joyneri* by Deischl (1964). In a study of intrageneric variation of

Mesodma, Novacek and Clemens (1977) found that *M. thompsoni* and *M. formosa* at the Bug Creek Anthills locality could not be distinguished on the basis of dentitions; our referrals of postcranial elements to this taxon are therefore designated as ?*Mesodma* sp.

7) Mantua Quarry, early Paleocene (Puercan), Fort Union Formation, Wyoming. Isolated calcaneum (PU 14487) of an unidentified multituberculate.

8) Uncertain locality in San Juan Basin, early Paleocene (Puercan), Nacimiento Formation, New Mexico. Ulnar fragment (AMNH 3036) of ?*Taeniolabis taoensis* (Cope, 1882a).

9) Locality 3 miles east of Kimbetoh, San Juan Basin, early Paleocene (Puercan), Nacimiento Formation, New Mexico. Nearly complete hind limbs and pelvis (AMNH 16325) of ?*Eucosmodon* sp. (Granger, 1915; Simpson

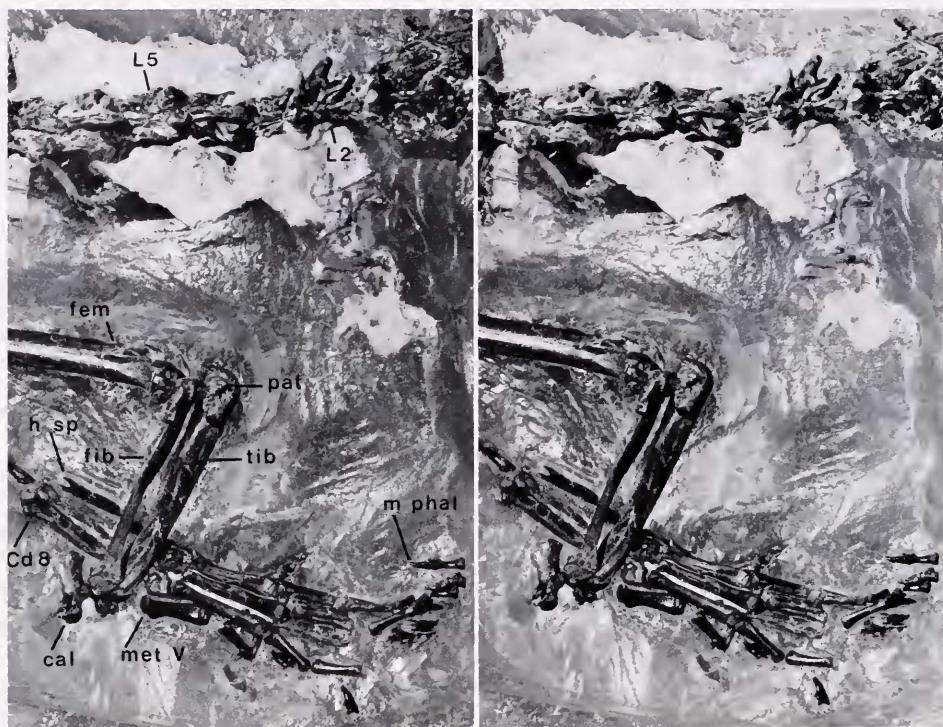


Figure 7. Stereophotographs of central portion of right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). For details of the right tarsal bones, see Figure 27A. $\times 1.25$.

Abbreviations: cal, calcaneum; Cd8, eighth caudal vertebra; fem, femur; fib, fibula; h sp, haemal spine; L2, L5, second and fifth lumbar vertebrae; m phal, manual phalanges; met V, fifth metatarsal; pat, patella; tib, tibia.

and Elftman, 1928; Granger and Simpson, 1929; Simpson, 1937a).

- 10) Torrejon Arroyo, San Juan Basin, middle Paleocene (Torrejonian), Nacimiento Formation, New Mexico. Associated dentaries and skeletal fragments (AMNH 16024) of *Stygimys teilhardi* (Granger and Simpson, 1929).
- 11) Gidley Quarry, middle Paleocene (Torrejonian), Fort Union Formation, Montana. Skull and several associated skeletal fragments (AMNH 35490) of *Ptilodus montanus* (Simpson, 1937b) and a left proximal humerus (USNM 9735) of ?*Ptilodus montanus*.
- 12) Silberling Quarry, middle Paleocene (Torrejonian), Fort Union Formation, Montana. Skull, dentaries and incomplete skeleton (USNM 6076) of *Ptilodus montanus* (Gidley, 1909; Simpson, 1937a,b).
- 13) Locality UAR2g, late Paleocene (Tiffanian), Ravenscrag Formation, Saskatchewan. Several isolated fragments (UA collections) of ?*Ptilodus kummae*.
- 14) UM locality SC-195, early Eocene (Clarkforkian), Willwood Formation, Wyoming. Associated dentition and skeletal fragments (UM 69868) of *Ectypodus powelli*.
- 15) UM locality SC-188, early Eocene (Clarkforkian), Willwood Formation, Wyoming. Isolated elements (UM collections) of unidentified multituberculate(s).
- 16) UM locality SC-210, early Eocene



Figure 8. Stereophotographs of posterior portion of right side of postcranial skeleton of *Ptilodus kummae* (UA 9001). $\times 1.25$. Abbreviations: l, left; r, right; Cd1, Cd7, first and seventh caudal vertebrae; fem, femur; fib, fibula; h sp, haemal spines; ilm, ilium; isc, ischium; S4, fourth sacral vertebra.

(Wasatchian), Willwood Formation, Wyoming. Humeral fragment (UM 74674) of *?Ectypodus tardus*.

OSTEOLOGY OF THE APPENDICULAR SKELETON

SCAPULOCORACOID

(Figures 9, 10)

UA 9001—A fragment of the right scapulocoracoid preserves most of the glenoid but little of the blade; the coracoid is broken off (Fig. 9B). The glenoid is a shallow, pyriform fossa, broadest posteriorly and tapering toward the coracoid suture.

On the costal surface of the scapula is a low crest that arises near the medial rim

of the glenoid fossa and extends postero-dorsally for approximately 3 mm. A shallow fossa and nutrient foramen occur on the posteromedial aspect of the blade adjacent to the glenoid.

Other material—*?Mesodma* sp. (UA 11992), distal fragment; *?Mesodma* sp. (UA 11993), distal fragment lacking coracoid process; Multituberculata indet. (MCZ 20785), distal fragment lacking coracoid process and scapular spine; Multituberculata indet. (UMVP 1400), distal fragment lacking coracoid process and scapular spine.

UA 11992 has a complete coracoid (Fig. 10C,D) that is synostosed to the scapula; no suture can be seen. Distally, the coracoid is transversely expanded to a slight degree. The scapular and coracoid parts of the glenoid thus form an arcuate (approximately 90°) surface to receive the humeral head.

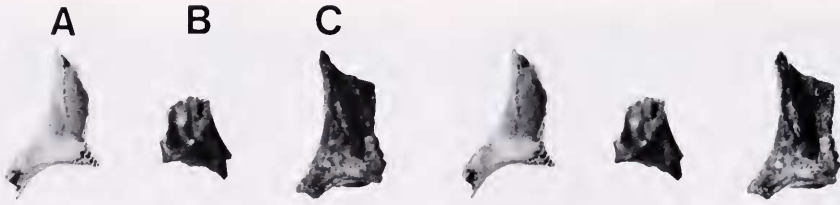


Figure 9. Stereophotographs of scapulocoracoids of North American Multituberculata. A) MCZ 20785, *Multituberculata* indet., Bug Creek Anthills locality, left distal fragment missing coracoid process, lateral view; B) UA 9001, *Ptilodus kummae*, locality UAR2g, right distal fragment missing coracoid process, lateral view; C) UMVP 1400, *Multituberculata* indet., Bug Creek Anthills locality, left distal fragment missing coracoid process, lateral view. $\times 2.2$.

The narrow scapular blade is partially preserved in several specimens from the Late Cretaceous (Figs. 9A,C, 10). The infraspinous fossa occupies the lateral surface as a deep sulcus. The anterior margin of the sulcus is a laterally projecting flange, the homologue of the scapular spine. In one specimen (UA 11992) the ventral (acromial) part of the spine is reflected

posteriorly, probably relating to the attachment of the deltoid. The acromion is not preserved in any available specimen.

CLAVICLE AND INTERCLAVICLE

No clavicle or interclavicle of a multituberculate has been positively identified. The fragmentary interclavicle (YPM

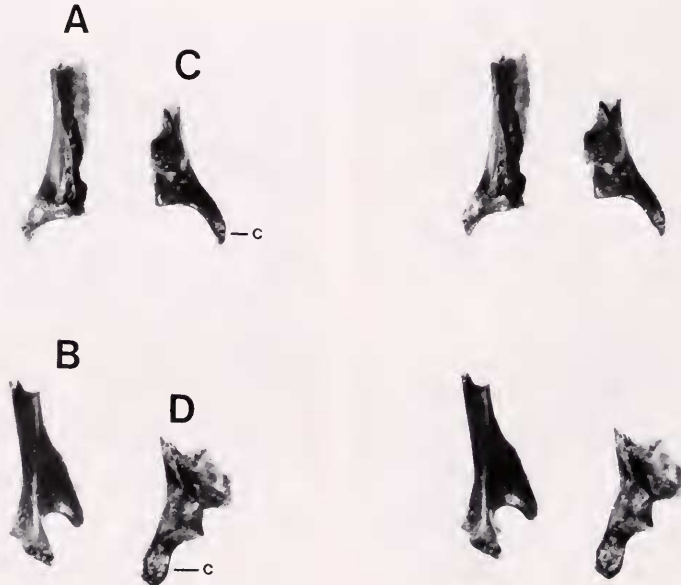


Figure 10. Stereophotographs of scapulocoracoids of ?*Mesodma* sp., Bug Creek Anthills locality. A) and B) UA 11993, left distal fragment missing coracoid process in lateral and anterior view; C) and D) UA 11992, right distal fragment in lateral and posterior views (in this specimen the coracoid process (c) is complete). $\times 4.0$.

10639) described by Marsh (1889) is enigmatic. The specimen's supposed association with a calcaneum, astragalus, and partial scapulocoracoid has been questioned (Simpson, 1928a,b; McKenna, 1961). McKenna (1961) provisionally referred the scapulocoracoid to the Marsupialia, and we find that the calcaneum and especially the astragalus differ in major features from the pattern known in *Ptilodus* and *?Eucosmodon* (see below). We do not doubt that the specimen in question is an interclavicle, but without comparative material have no basis for confirming or denying that it represents that of a multituberculate.

HUMERUS

(Figures 11, 12)

UA 9001—The humeri are represented by fragments from the heads, a partial right diaphysis, and a fragment of the distal end of the right humerus.

The large and spherical radial condyle (capitulum) is ventrally directed. Dorsal to the condyle is a broad linear ridge that runs proximodistally and forms the lateral margin of the intercondylar groove. Ventrally, a shallow groove separates the radial condyle from the ectepicondyle. The ulnar condyle, separated from the radial condyle by the wide intercondylar groove, is elongate and wraps around the distal end of the humerus. The extensor (dorsal) surface is situated more laterally than the flexor surface, and thus has a "spiral" configuration (Jenkins, 1973).

Other Material—*?Catopsalis joyneri* (MCZ 19529), right distal fragment; *?Cimexomys minor* (UMVP 1404), left distal fragment; *?Ectypodus tardus* (UM 74674), right distal fragment; *?Meniscoessus conquistus* (AMNH 3011a), left distal fragment; *?Meniscoessus robustus* (YPM 10612a), left distal fragment; *?Mesodma primaeva* (AMNH 77175), right distal fragment; *?Mesodma* sp. (MCZ 20789), left distal fragment; *?Mesodma* sp. (MCZ 20786, MCZ 20787, MCZ 20788, UMVP 1405, UMVP 1406), right distal fragments; *?Mesodma* sp. (UMVP 1403), distal two-thirds of left humerus; *?Ptilodus kummae* (UA

11300), right distal epiphysis; *Ptilodus montanus* (USNM 6076), nearly complete but damaged left humerus; *?Ptilodus montanus* (USNM 9735), left proximal humerus; *?Stygimys kuszmauli* (UA 11994), distal half of right humerus; *?S. kuszmauli* (UMVP 1407), left distal humerus; *?Stygimys teilhardi* (AMNH 16024), right radial condyle.

The best preserved proximal humerus of a North American form is problematical in its association; the specimen was found in the same box with a maxilla (USNM 9735) of *Ptilodus montanus* from Gidley Quarry, but no records attest to its actual association. That it is multituberculate is established by its resemblance to the proximal humerus of *Tugrigbaatar saichanensis* figured by Kielan-Jaworowska and Dashzeveg (1978). The specimen possesses robust greater and lesser tuberosities and a bulbous, ovoid head that is reflected proximodorsally (Fig. 11A,B,C).

The linear ulnar condyle, in distal view, intercepts the interepicondylar axis at an angle of approximately 72° on the humeral fragment of *?Ptilodus kummae* (UA 11300) as well as on that of *P. montanus* (USNM 6076). The entepicondyle is not preserved on either UA 9001, UA 11300, or USNM 6076, but a distinct groove separates it from the ulnar condyle. More nearly complete humeri of multituberculates recovered from the Bug Creek Ant-hills locality in UMVP and UA collections show that the entepicondyle is much larger than the ectepicondyle; the entepicondyle projects distomedially as a broad, dorsoventrally depressed flange and is pierced by a large entepicondylar foramen (see also Jenkins, 1973, fig. 19).

A complete humerus is not known for any North American multituberculate. The most complete specimen available (*Ptilodus montanus*, USNM 6076; Fig. 11H,I) reveals a well-developed deltopectoral crest and a nearly hemispherical humeral head (breakage precludes determining its exact orientation). The lateral surface of the deltopectoral crest and the dorsal surface of the shaft have an angular intersection, thus forming a distinctive ridge running proximodistally from the

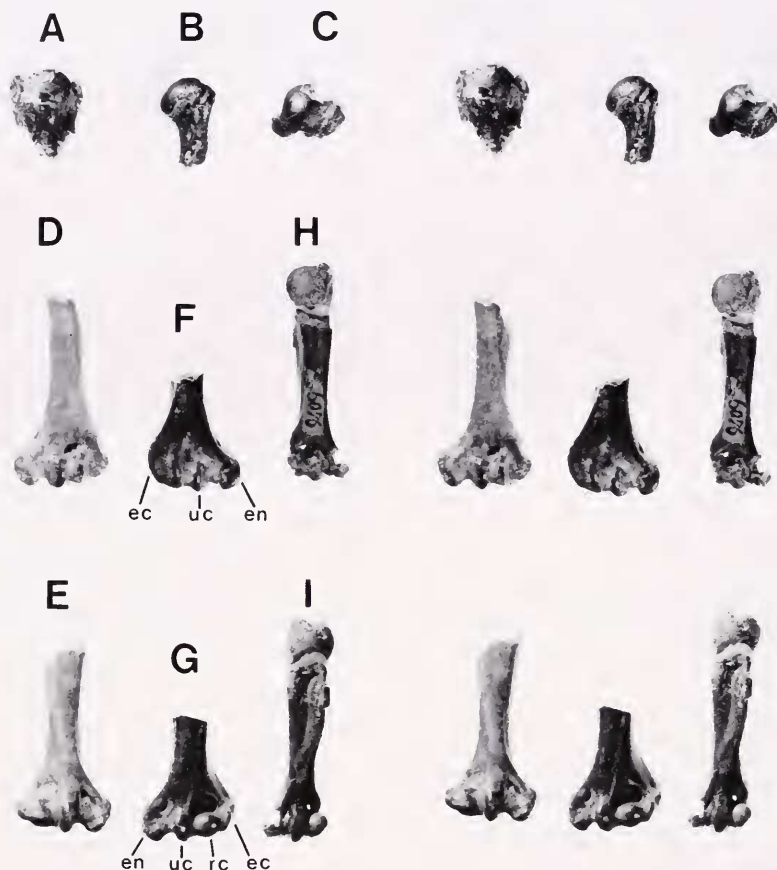


Figure 11. Stereophotographs of humeri of North American Multituberculata. A-C) USNM 9735, *?Ptilodus montanus*, Gidley Quarry, left proximal humerus in dorsal, medial and proximal views. The articular surface adjacent to the greater tuberosity has been damaged. D) and E) UA 11994, *?Stygimys kuszmauli*, Bug Creek Anthills locality, right distal fragment in dorsal and ventral views; F) and G) UMVP 1407, *?Stygimys kuszmauli*, Bug Creek Anthills locality, left distal fragment in dorsal and ventral views; H) and I) USNM 6076, *Ptilodus montanus*, Silberling Quarry, nearly complete but damaged left humerus (head is affixed with clay) in dorsal and ventral views. $\times 1.5$.

Abbreviations: ec, ectepicondyle; en, entepicondyle; rc, radial condyle; uc, ulnar condyle.

humeral head to the ectepicondylar flange (the "posterior crest" of Kielan-Jaworowska and Dashzeveg, 1978). The proportions of the humerus represented in Figure 31 are based in part on USNM 6076 in which the head is separated from the shaft; it is possible that part of the shaft has been lost at the fracture. A reconstruction of the humerus of *Tugrigaatar sai-*

chanensis by Kielan-Jaworowska and Dashzeveg (1978) depicts a more gracile, elongate bone.

ULNA (Figures 13, 14)

UA 9001—The right ulna is represented by a fragment representing the olec-

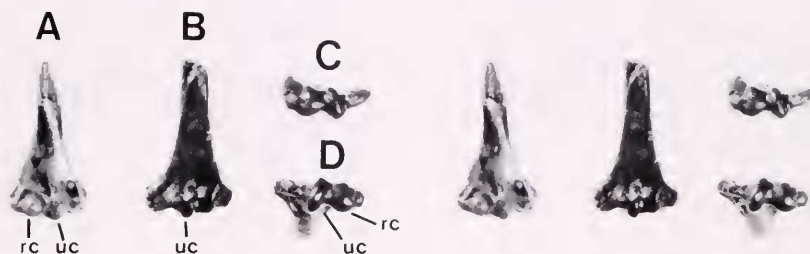


Figure 12. Stereophotographs of humeri of *Mesodma* sp., Bug Creek Anthills locality. A) MCZ 20788, right distal fragment, ventral view; B) MCZ 20787, right distal fragment, dorsal view; C) MCZ 20789, left distal fragment, distal view; D) MCZ 20786, right distal fragment, distoventral view. $\times 3.0$.

Abbreviations: rc, radial condyle; uc, ulnar condyle.

ranon and proximal part of the semilunar notch (Fig. 13B).

The olecranon is laterally compressed. The medial margin of the apex bears an excrescence, and therefore the olecranon is somewhat asymmetrical. The articular surface for the capitulum is a shallowly concave facet restricted to the dorsolateral corner of the semilunar notch. The articular surface for the ulnar condyle is nearly semicircular; proximally, the facet is deeply recessed, but distally is almost flat

from medial to lateral side. The proximodistal axis of this facet is obliquely oriented (estimated at about 10°) to the ulnar shaft. A prominent crest is formed at the intersection of the two facets and is also oriented slightly obliquely to the axis of the ulnar shaft (from proximolateral to distomedial aspect); it articulates with the intercondylar groove on the humerus. A prominent anconeal process is accommodated by a deep olecranon fossa on the humerus.

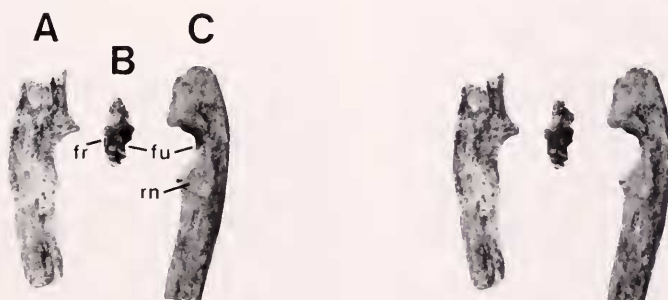


Figure 13. Stereophotographs of ulnae of North American Multituberculata. A) UMVP 1412, *Catopsalis joyneri*, Bug Creek Anthills locality, left proximal fragment missing part of olecranon process, anteromedial view; B) UA 9001, *Ptilodus kurpmiae*, locality UAR2g, right proximal fragment, anterior view; C) MCZ 19527, *Catopsalis joyneri*, Bug Creek Anthills locality, left proximal fragment missing part of olecranon process, lateral view. $\times 1.5$.

Abbreviations: fr, facet for radial condyle; fu, facet for ulnar condyle; rn, radial notch.

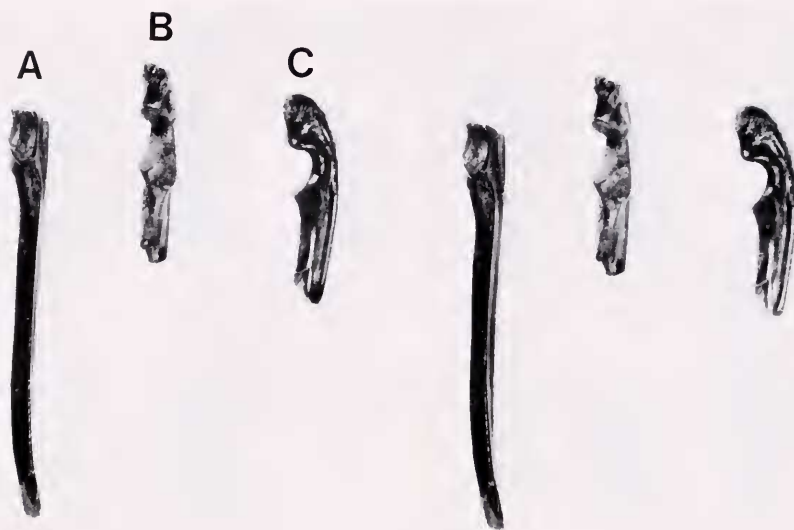


Figure 14. Stereophotographs of ulnae of *Mesodma* sp., Bug Creek Anthills locality. A) UMVP 1414, right ulna missing proximal and distal ends, anterior view; B) MCZ 20780, left proximal fragment, anterior view; C) MCZ 20781, left proximal fragment, lateral view. $\times 4.2$.

Other Material—*Ptilodus kummae* (UA 11302), distal half of semilunar notch and proximal part of shaft; *Stygimys teilhardi* (AMNH 16024), two olecranons including proximal half of semilunar notch; *S. kuszmauli* (UMVP 1411), proximal right ulna; *Mesodma* sp. (UMVP 1413), left semilunar notch and olecranon; *Mesodma* sp. (UMVP 1409), proximal right ulna; *Mesodma* sp. (UMVP 1410), proximal right ulna; *Mesodma* sp. (UMVP 1414), distal half of semilunar notch and all of shaft except distal end; *Mesodma* sp. (MCZ 20780, MCZ 20781), left proximal fragments; *Catopsalis joyneri* (UMVP 1412), proximal half of left ulna; *Catopsalis joyneri* (MCZ 19527), proximal left ulna missing part of olecranon; *Cimexomys minor* (UMVP 1408), semilunar notch of left ulna; *Taeniolabis taoensis* (AMNH 3036), semilunar notch of right ulna.

The radial notch is an oval, shallowly concave facet distal to the articular surface for the radial condyle.

Distal to the semilunar notch the ulnar shaft narrows transversely. A longitudinal fossa, bordered medially by a ridge, occurs on the flexor surface of the shaft just distal to the coronoid process.

An ulnar shaft (UMVP 1414) referable to *Mesodma* sp. has a cross section in the

form of an isosceles triangle, with the base representing the anterior surface and the apex the posterior margin (Fig. 14A). Distally the shaft curves medially, tapers, and becomes more or less cylindrical. A distal articular surface has not yet been positively identified.

RADIUS (Figure 15)

UA 9001—The radii of *P. kummae* are represented by the head from the left side, and the proximal half from the right. Associated with the ?right carpus is a crushed distal radius that preserves no diagnostic features.

The head of the radius is elliptical in outline. The concave capitular facet is also elliptical, that is, longer anteroposteriorly than transversely. However, the concavity of the articular surface is spheroidal. A strap-shaped facet that articulates with the

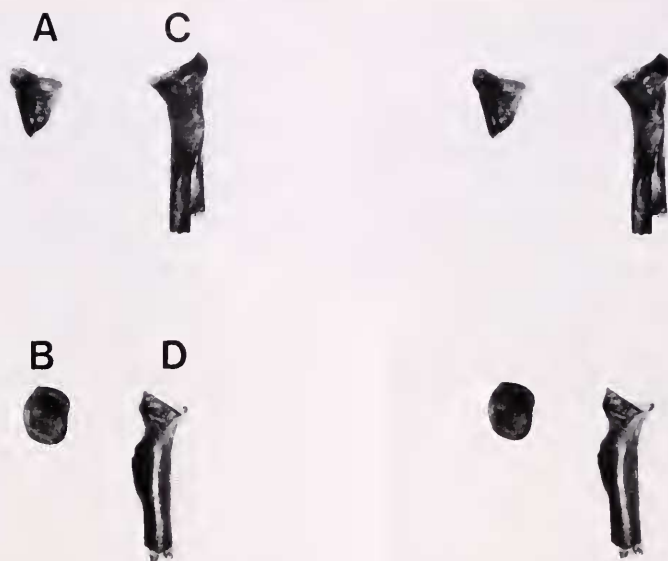


Figure 15. Stereophotographs of radii of *Ptilodus kummae* (UA 9001), locality UAR2g. A) and B) left proximal fragment in medial and proximal (top is posterior) views; C) and D) right proximal fragment in medial and lateral views. $\times 2.7$.

ulna extends for approximately 90° around the posteromedial margin of the radial head. The anterolateral margin of the radial head bears an elongate, flat facet that opposes a shallow groove between the ectepicondyle and the radial condyle of the humerus.

The proximal part of the shaft is mediolaterally compressed. Distal to the ulnar facet is a longitudinal ridge, the anterior surface of which is rugose and probably marks the insertion of the biceps brachii. The angular anteromedial margin of the shaft may represent the attachment of a radioulnar interosseous membrane.

Other Material.—? *Mesodma* sp. (UMVP 1416), proximal half of right radius; ? *Catopsalis joyneri* (UMVP 1438, UMVP 1439), proximal halves of left radii; *Ptilodus montanus* (USNM 6076), right radius lacking distal end.

These specimens share the same basic features with the proximal radii of *Ptilodus kummae*.

MANUS

(Figures 3, 6, 16)

UA 9001.—A partial and slightly disarticulated manus is preserved (Fig. 16). The interpretation that it is a right manus, and the identification of the individual ossicles, are not absolutely certain. The single complete metacarpal (5.3 mm in length) we regard as pollical, and on this assumption have been able to suggest the identity of the other elements. This interpretation is based on three observations: the pollical metacarpal appears to be associated with two phalanges only; the pollical metacarpal is in articulation with another metacarpal (II?) at a greater angle of divergence (ca. 40°) than would be expected if it were metacarpal V of the left side; and the adjacent ossicle (prepollex), although elongate, is too small and of an unlikely structure for a pollical metacarpal (see below).



Figure 16. Stereophotographs of dorsal view of partial ?right manus of *Ptilodus kummae* (UA 9001). $\times 4.4$.

Abbreviations: *d phal*, distal phalanx; *mag*, magnum; *met I, II*, first and second metacarpals; *prp*, prepollex; *p phal*, proximal phalanx; *sml*, semilunar; *tzd*, trapezoid; *tzm*, trapezium.

As preserved, the carpus consists of a damaged distal radius, semilunar (lunate), magnum (capitate), trapezoid, trapezium, and prepollex. The semilunar is a crescentic ossicle, with a concave distal articular surface lying in close contact with the bulbous head of the magnum. The trapezoid is displaced from the magnum, but when articulated their proximal surfaces would be contiguous. Distally, the trapezoid articulates with metacarpal I and a lateral portion of the proximal articular surface of metacarpal II. The trapezium, roughly equivalent to the trapezoid in size, has been displaced from its normal position. The elongate prepollex (2.8 mm in length) is expanded at both ends and appears to have articulated with both the trapezium and pollical metacarpal. The long axes of the proximal and distal ends are at nearly right angles. The distal end, although rounded, does not have the condylar shape typical of a metacarpophalangeal articulation.

The proximal end of metacarpal II is transversely narrower, and its shaft more slender, than that of the pollical metacarpal.

The distal (ungual) and proximal phalanges of the right pollex appear to be associated (Fig. 16). The proximal phalanx is 2.6 mm long and, at midshaft, is 1.1 mm in width. Both the proximal base and, to a lesser extent, the distal end are expanded relative to the transverse diameter of the shaft. The base is dorsoventrally expanded. The head, in dorsal profile, is very slightly convex, bearing no median groove.

The distal phalanx, 2.4 mm long, has a proximal facet that is deeply concave in side view. Both the extensor process and the flexor tubercle are well developed. The flexor tubercle is low, rounded, and is separated from the articular surface by a fossa into which opens a large, distally directed nutrient foramen. The ungual process for support of the claw is slightly recurved and bears a longitudinal, often

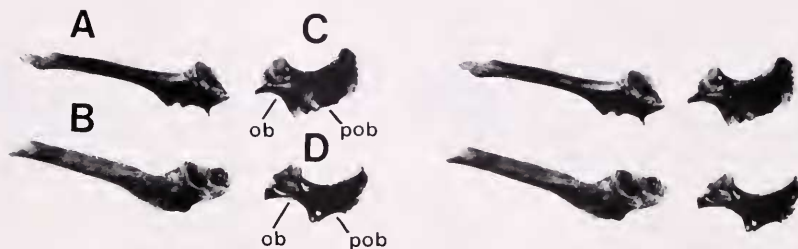


Figure 17. Stereophotographs of pelvic bones of ?*Mesodma* sp., Bug Creek Anthills locality. A) UMVP 1418, partial left ilium, lateral view; B) UMVP 1420, partial left ilium and acetabular facet of the ischium, lateral view (in both specimens part of the pubis is represented along the inferior margin of the acetabulum); C) UMVP 1419, left ischial fragment, lateral view; D) UMVP 1417, left ischial fragment, lateral view. $\times 2.2$.

Abbreviations: ob, dorsal margin of obturator foramen; pob, dorsal margin of postobturator foramen.

rugose groove along its dorsomedial and dorsolateral aspects (the dorsolateral groove is longer and deeper). The ungual process is slightly constricted transversely near midlength, expands distally, and tapers to a pointed terminus.

Three middle and three distal phalanges of the ?left manus are preserved in articulation near the distal end of the right pes (Figs. 4, 7). Their digital identity cannot be determined. They are similar in morphology to the pollical phalanges described above but are of different lengths.

PELVIS

(Figures 5, 8, 17, 18)

UA 9001—Both ilia and the left ischium of *UA 9001* are preserved intact; the right ischium and both pubes are crushed (Figs. 5, 8). Pelvic sutures appear to have been firmly synostosed.

The long, rodlike ilium is reflected laterally at its anterior end. The ilium is elliptical in cross-section except at the expanded auricular surface and adjacent to the anterior rim of the acetabulum where it is blade-like. The ventral margin of the ilium adjacent to the acetabulum bears a flange that merges with the pubis below.

The lateral surface of the ischium is flat, the medial surface convex. The dorsal margin, rather than straight, recurves sharply to a dorsally directed ischial tuberosity. Although the acetabula are obscured by the articulated femoral heads, the superior margin is recessed and open dorsally by virtue of a lack of contact between the iliac and ischial facets.

Distortion of both pubes and the right ischium, and the fact that the ventral part of the left ischium is almost completely covered by overlying bone, obscures the obturator region. However, it appears that posterior to the obturator foramen lies another, smaller foramen, hereafter referred to as the postobturator foramen.

The obturator foramen is situated directly ventral to the acetabulum, its anterior margin lying at approximately the same level as the anterior margin of the acetabulum. Ventrally, it appears to have been bounded by a thin lamina of bone that is not preserved in any other multituberculate specimen. Deformation precludes precise measurement of the foramen although in anteroposterior length it appears to have been close to 4 mm.

The postobturator foramen is separated from the obturator foramen by a plate of bone approximately 2 mm wide (anteroposteriorly). The foramen itself is approx-

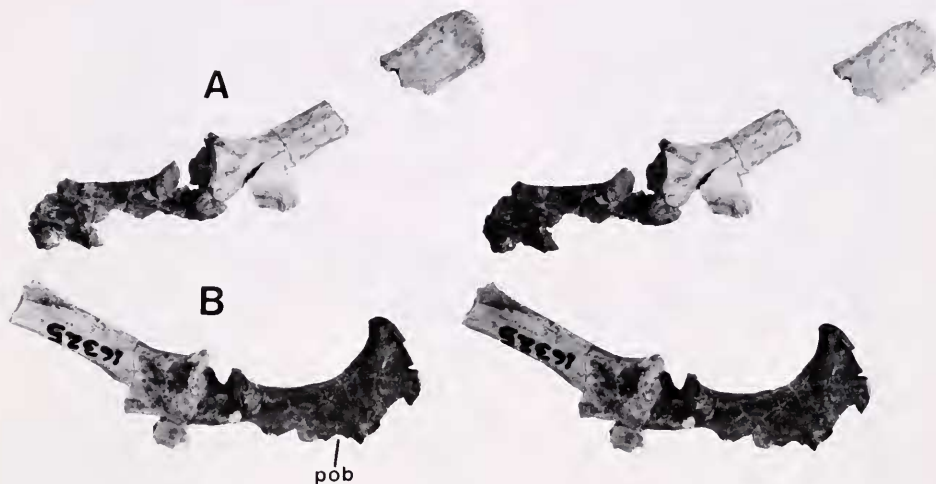


Figure 18. Stereophotographs of pelvis of *?Eucosmodon* sp. (AMNH 16325), San Juan Basin. A) fragmentary right ilium and ischium, lateral view; B) fragmentary left ilium and ischium, lateral view. $\times 1.25$.

Abbreviations: pob, dorsal margin of postobturator foramen.

imately 2.5 mm wide and about 2 mm high; although breakage has occurred, it appears to have been bordered ventrally by a very thin lamina of bone. The post-obturator foramen does not open into the pelvic cavity, but rather represents a hiatus in a keel-like ischio-pubic symphysis.

The pubis forms the anterior and part of the ventral border of the obturator foramen. Details of its shape, including the possible presence of facets for epipubic bones, have been lost by postmortem crushing and breakage.

Two elongate, boomerang-shaped bones are located near the right ilium and left ischium, respectively. One end tapers, the other terminates in a slight swelling. A longitudinal sulcus traverses the length of one side of the shaft. These features are similar to those characteristic of the bones that Jenkins and Parrington (1976) identified tentatively as the clavicles of *Eozostrodon*. The possibility that these are clav-

icles appears to be remote because no other elements of the anterior limb skeleton of *Ptilodus* were so displaced. Rather, it is likely that these are epipubes, and that Jenkins and Parrington's identification may be in error.

Other Material—*?Eucosmodon* sp. (AMNH 16325), nearly complete pelvis including parts of both ilia and ischia, the pubes represented only by bone in region of iliopubic junction; *?Mesodma* sp. (UMVP 1419), partial left ischium; *?Mesodma* sp. (UMVP 1420), nearly complete left ilium lacking anterior tip of blade but including entire acetabulum; *?Mesodma* sp. (UMVP 1417), partial left ischium; *?Mesodma* sp. (UMVP 1418), nearly complete left ilium preserving iliac facet of acetabulum and part of auricular surface; *Ptilodus montanus* (USNM 6076), fragmentary left ilium; *Stygimys teilhardi* (AMNH 16024), right iliac fragment preserving iliac facet.

The acetabular articular surface, unlike that of therian mammals, is highly asymmetrical. The anterior and largest part of the surface is made up of iliac and pubic contributions; the sutural contacts are



Figure 19. Stereophotographs of femora of North American Multituberculata. A) UA 11301, *?Ptilodus kummae*, locality UAR2g, left proximal fragment, proximal view; B) AMNH 16024, *Stygimys teilhardi*, Torrejon Arroyo, right distal fragment, distal view. $\times 2.1$.

Abbreviations: fov, fovea capitis femoris.

obliterated in UMVP 1420, but a slight indentation of the acetabular margin and different textural features of the articular surface are here interpreted as marking the iliopubic junction (Fig. 17B). The superior margin of the acetabulum between the ilium and ischium is deeply emarginated. An acetabular fossa and notch are well developed. Similar features are present in *?Eucoosmodon* sp. (AMNH 16325) although details are obscured by breakage (Fig. 18).

Further evidence for a postobturator foramen is evident in UMVP 1419 and UMVP 1417 (Figs. 17C,D), where the dorsal margins of both the obturator and postobturator foramina are separated by a cylindrical bony rod of small diameter. The ventral margins of neither foramen are preserved, however. In AMNH 16325 the dorsal margins of both the obturator and the postobturator foramina are also present. In both *?Eucoosmodon* sp. (AMNH 16325) and *?Mesodma* sp. (UMVP 1419 and 1417) the postobturator foramen is developed within the ischial part of the ischiopubic symphysis and thus is an unpaired, midline feature. Whether or not the foramen had a bony ventral margin as appears to have been the case in *Ptilodus kummae*, or was a hemicircular incisure of the ischial rami, cannot be determined from available materials.

Association of the foramen with the origin of an adductor muscle is indicated by the surrounding fossa on the lateral surface (Fig. 17C,D).

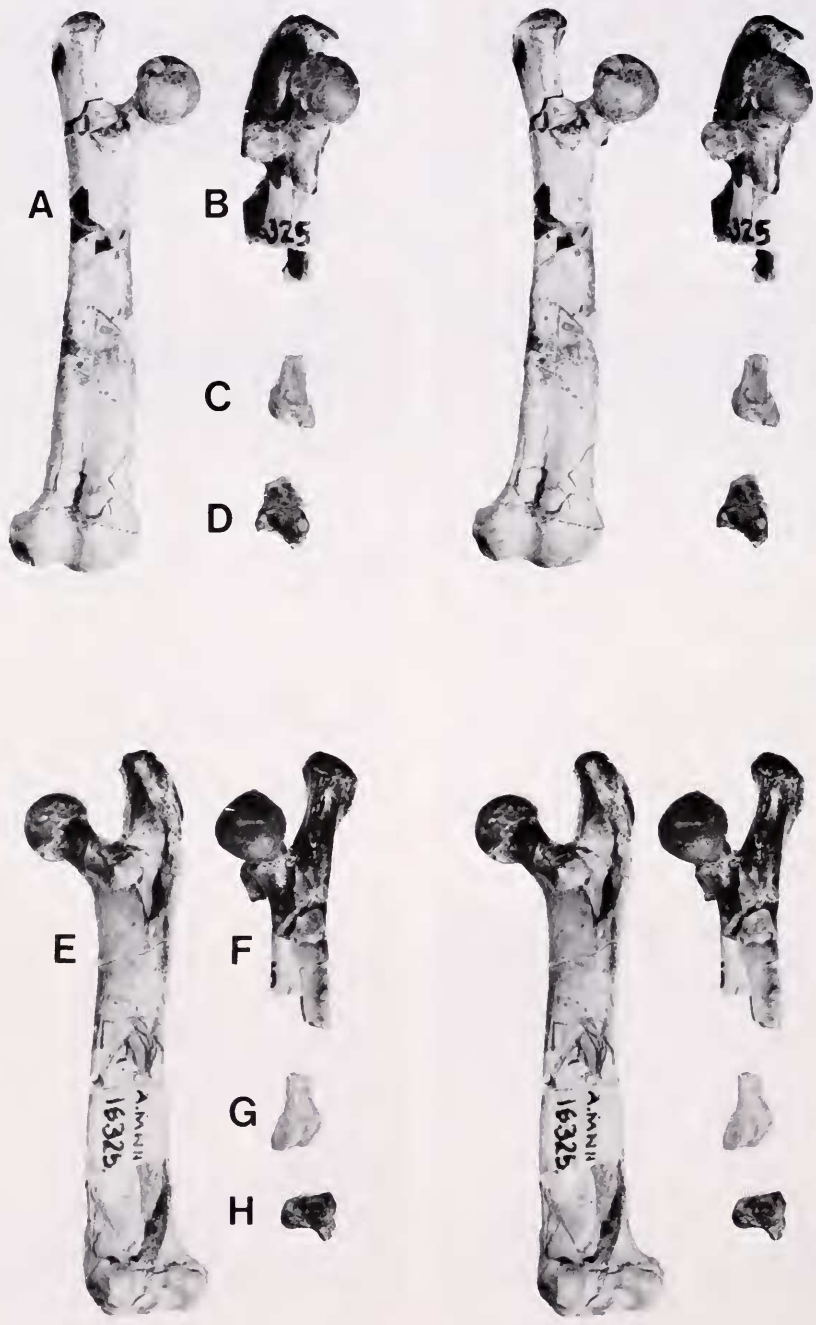
The indentation along the ventral margin of the ischium of *Kryptobaatar dashzevegi* posterior to the obturator foramen may represent a postobturator foramen (Kielan-Jaworowska, 1969: fig. 1A; 1979: fig. 1a,b). A characteristic feature of *K. dashzevegi* and other Mongolian multituberculates from which nearly complete, uncrushed pelvises are known is that the ischiopubic symphysis is formed at an acute angle and extends ventrally as a distinct keel (Kielan-Jaworowska, 1979). As far as can be determined from available materials, North American multituberculates shared the same feature.

FEMUR

(Figures 4, 5, 7, 8, 19, 20A,B,E,F, 21)

UA 9001—The articular surface of the femoral head is slightly greater than hemispherical, more so than indicated for *Ptilodus montanus* by Gidley (1909: fig. 5). The dorsally reflected head is well set off by a cylindrical neck that joins the shaft at an angle of about 60° (Figs. 5, 8).

The robust greater trochanter extends



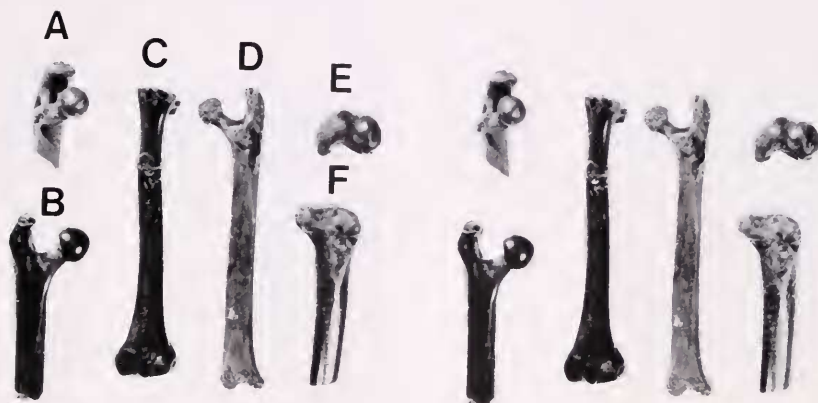


Figure 21. Stereophotographs of femora of ?*Mesodma* sp., Bug Creek Anthills locality. A) MCZ 20775, left proximal fragment, ventromedial view; B) UMVP 1423, right proximal fragment, dorsal view; C) UMVP 1424, right femur missing proximal end, dorsal view; D) MCZ 20776, right femur missing distal epiphysis, ventral view; E) MCZ 20777, left distal femur, distal view; F) MCZ 20778, right distal femur, ventral view. $\times 2.2$.

along the axis of the shaft well above the level of the head. The expanded apex bears a large, rugose area for insertion of gluteal musculature. Distally, the insertion area is prolonged along the ventrolateral aspect of the shaft as a sharp (gluteal) crest. The digital fossa is small and narrow. The bulbous lesser trochanter, approximately one-third the size of the femoral head, projects ventrally and is a simple rounded eminence. A second fossa, between the lesser trochanter medially and the gluteal crest laterally, may be part of a divided digital fossa (Simpson and Elftman, 1928).

The shaft is circular in cross section at midlength but more elliptical proximally.

The junction between the shaft and the distal epiphysis of the femur is clearly marked. The patellar groove crosses the distal end obliquely from proximomedial

to distolateral aspect and terminates dorsal to the lateral condyle. The two condyles are separated by a broad intercondyloid fossa. The facets have a large radius of curvature (i.e., are relatively flat) and are confined to the ventral aspect of the condyles. The lateral condyle, wider but less protuberant than the medial condyle, bears a shallow, round fossa adjacent to the lateral ridge of the patellar groove.

Other Material.—?*Catopsalis joyneri* (UMVP 1427), left proximal fragment; ?*Cimexomys minor* (UMVP 1421), left proximal fragment; ?*Eucosmodon* sp. (AMNH 16325), complete right femur and left proximal fragment; ?*Meniscoessus robustus* (YPM 10625c), right proximal fragment; ?*Mesodma primaeva* (AMNH 77178), right proximal fragment; ?*Mesodma* sp. (UMVP 1422, 1423), right proximal fragments; ?*Mesodma* sp. (MCZ 20775), left proximal fragment; ?*Mesodma* sp. (MCZ 20776), right femur lacking distal epiphysis; ?*Mesodma* sp. (UMVP

Figure 20. Stereophotographs of femora and fibulae of ?*Eucosmodon* sp. (AMNH 16325), San Juan Basin. A) right femur, dorsal view; B) left proximal femur, ventromedial view; C) right distal fibula, posteromedial view; D) left distal fibula, distomedial view; E) right femur, ventral view; F) left proximal femur, dorsomedial view; G) right distal fibula, anterolateral view; H) left distal fibula, distal view (top is medial). $\times 1.2$.

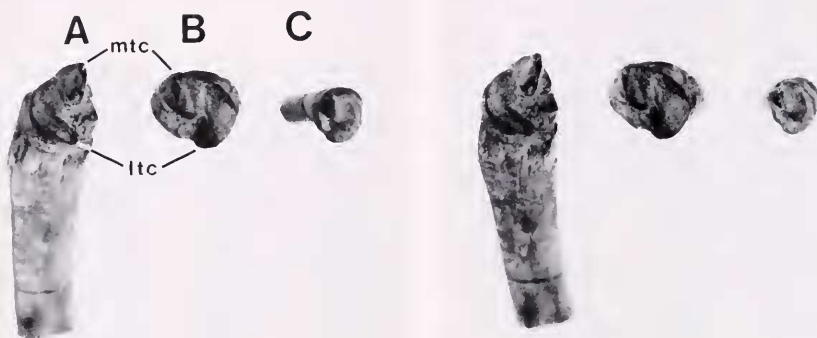


Figure 22. Stereophotographs of tibiae of North American Multituberculata. A) AMNH 16325, ?*Eucosmodon* sp., San Juan Basin, right distal fragment, posterodistal view; B) AMNH 16325, ?*Eucosmodon* sp., San Juan Basin, left distal fragment, distal view (top is anterior); C) AMNH 16024, *Stygimys teilhardi*, Torrejon Arroyo, left distal fragment, distal view (top is anterior). $\times 1.5$.

Abbreviations: *ltc*, lateral tibial condyle; *mtc*, medial tibial condyle.

1424), right femur lacking head and greater trochanter; ?*Mesodma* sp. (MCZ 20777), left distal femur, and (MCZ 20778) right distal femur; ?*Ptilodus kummae* (UA 11301), left femoral head and greater trochanter; *Ptilodus montanus* (AMNH 35490), right femur lacking distal end and left femur lacking head and distal end; *P. montanus* (USNM 6076), right femur lacking distal end; ?*Stygimys kuszmauli* (UMVP 1425), right proximal fragment; ?*S. kuszmauli* (UMVP 1426), left femoral shaft; *Stygimys teilhardi* (AMNH 16024), left greater trochanter and right distal fragment.

The multituberculate femoral head exhibits a heart-shaped, somewhat flattened and slightly rugose area representing the fovea capitis femoris (Fig. 19A). The fovea, eccentrically situated on the ventral aspect of the femoral head, marks the point of attachment of the ligamentum capitis femoris.

Specimens of ?*Eucosmodon* sp. (AMNH 16325) and ?*Stygimys kuszmauli* (UMVP 1426) reveal crests running distally along the ventrolateral aspect of the shaft from the greater and lesser trochanters respectively.

The patellar groove of ?*Mesodma* sp. (UMVP 1424 and MCZ 20777) extends proximally past the epiphyseal junction and well onto the dorsal aspect of the shaft (Fig. 21C,E). The obliquity of the groove, as well as its location on the lateral side of the epiphysis, is evident in these specimens.

PATELLA

(Figure 7)

UA 9001—The right patella is a small, elliptical bone preserved on the lateral condyle of the tibia. Although somewhat crushed, it appears to have been concave along the articular surface, and convex along the dorsal surface.

TIBIA

(Figures 4, 5, 7, 22, 23A-E, 27)

UA 9001—The proximal end is markedly asymmetric. Medially the small,

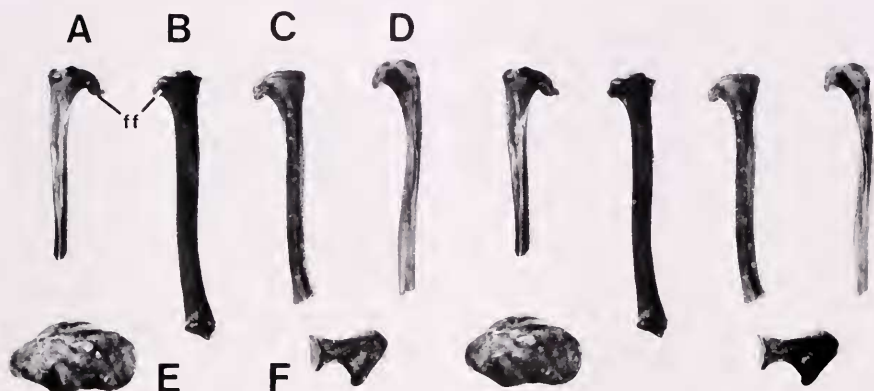


Figure 23. Stereophotographs of tibiae and parafibula of North American Multituberculata. A) MCZ 20779, ?*Mesodma* sp., Bug Creek Anthills locality, right proximal tibia, posterior view; B) UMVP 1428, ?*Mesodma* sp., Bug Creek Anthills locality, left tibia, posterior view; C) UCMP 122048, ?*Mesodma* sp., Bug Creek Anthills locality, right proximal tibia, anterior view; D) UA 11995, ?*Mesodma* sp., Bug Creek Anthills locality, left proximal tibia, posteromedial view; E) UMVP 1429, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, left proximal tibia, proximal view (top is anterior); F) UA 9001, *Ptilodus kummae*, locality UAR2g, parafibula, side view (articular facet is at left, muscular process is at right; other details of this bone's orientation are unknown). $\times 2.2$.

Abbreviations: ff, fibular facet.

slightly depressed concave facet for the medial femoral condyle is ovoid in outline; its long axis is oriented anterolaterally-posteromedially. The lateral facet is larger and its long axis is oriented transversely; the surface is saddle-shaped, convex anteroposteriorly and concave mediolaterally. The intercondyloid eminence is higher posteriorly than anteriorly. A large, hook-like flange descends distally from the posterolateral corner of the proximal end, and bears a facet on its posterior surface for the fibula. A thin lamina of bone joins the flange from the shaft of the tibia and, anteriorly, forms a shallow fossa between the two structures.

The anterior surface of the tibia is smooth and convex; there is no distinct tibial tuberosity. Posteriorly, the tibia is deeply excavated just below the proximal articular surface. The shaft bears a distinctly sigmoidal curvature; the proximal

half is bowed medially, the distal half laterally.

Two condyles are developed on the distal articular surface. The long axis of the oval medial condyle is oriented anteromedially-posterolaterally; the medial extremity of the condyle forms the distal tip of the bone. The spiral lateral condyle wraps around the medial facet. The two condyles are separated by a spiral groove that accommodates an oblique ridge between the two corresponding sulci on the astragalus.

Other Material.—?*Eucosmodon* sp. (AMNH 16325), proximal end of right tibia, distal ends of both tibiae; ?*Mesodma* sp. (UMVP 1428), complete left tibia; ?*Mesodma* sp. (MCZ 20779, UA 11995), right proximal fragments; ?*Stygimys kuszmauli* (UMVP 1429), right and left proximal fragments; *Stygimys teilhardi* (AMNH 16024), proximal and distal fragments; Multituberculata indet. (UMVP 6663), left tibia lacking distal end; Multituberculata indet. (UCMP 122048), right tibia lacking distal end;

Multituberculata indet. (UMVP 1641), right proximal fragment.

These tibiae reveal that the posterior fossa on the proximal end of the shaft completely undercuts much of the articular surface; the lateral articular facet and the intercondylar eminence are unsupported by bone except anteriorly. The most complete tibia (UMVP 1428) displays the characteristic sigmoidal curvature of the shaft; the proximal half is bowed medially, the distal half laterally. Features of the proximal articular surface are best exhibited on the slightly water-worn specimens of *?Styginys kuszmauli* (e.g., UMVP 1429). The distal end is best preserved in *?Eucosmodon* sp. (AMNH 16325) (Fig. 22A,B).

FIBULA

(Figures 4, 5, 7, 8, 20C,D,G,H, 27)

The fibula, previously poorly known in multituberculates, is preserved intact in both hind limbs of *Ptilodus kummae*. The precise orientation of the fibula, however, remains uncertain.

It appears that the large flat facet on the posterolateral margin of the tibial head articulated with a large, flat facet on the fibular head. If this interpretation is correct, the fibula was situated slightly posterior to the tibia proximally, but distally lay more lateral to it.

The left fibular head exhibits a large, convex facet along its posterior margin that articulated with the para-fibula (Fig. 8). The fibular head bears a long, slender reflected process that arises from its posterolateral margin and is directed distally. Owing to the anteroposterior alignment of the proximal end of the tibia and fibula the lateral flanges of those bones were also closely aligned in an anteroposterior relationship. Both the tibial and fibular processes appear to be related to a crural musculotendinous attachment.

The shaft of the fibula is cylindrical,

slender, bowed slightly posterolaterally at midlength, and expands distally to a large epiphysis. The distal epiphysis of the left fibula is separated from the diaphysis. Although the articular surfaces of both distal epiphyses are obscured by overlying bone, it is evident that the posteromedial surface is concave and articulated with a small ossicle (a ?lunula, see below) and that the lateral side is convex (Fig. 27). A tuberosity protrudes from the anterolateral margin of the epiphysis.

Although slight displacement of the articular relationships is evident, the right foot of *P. kummae* reveals that the distal end of the fibula articulated with the dorsolateral margin of the astragalus (Fig. 27).

Other Material—*?Eucosmodon* sp. (AMNH 16325), left and right distal fragments (Fig. 20C,D,G,H).

The distal end of the fibula is triangular in outline, with anterior, posteromedial, and posterolateral sides. A large, bulbous facet near the anteromedial side apparently represents the astragalar contact. A tuberosity occurs anterolaterally, and a small, prominent spine posteriorly. The distal fibula illustrated by Granger and Simpson (1929, Fig. 22C) is from the left side and is shown in posteromedial and distal views (not anterior and medial, as indicated).

PARAFIBULA

(Figure 23F)

UA 9001—A pair of ossicles found in association with the hind limbs are here interpreted as para-fibulae. Each bears a small, elliptical, concave articular surface that matches the large convex facet on the posterior surface of the proximal end of the fibula. A short, constricted neck separates the articular end from a blade-like muscular process that bears two distinct tuberosities along the margin. These para-fibulae are notable for their large size.

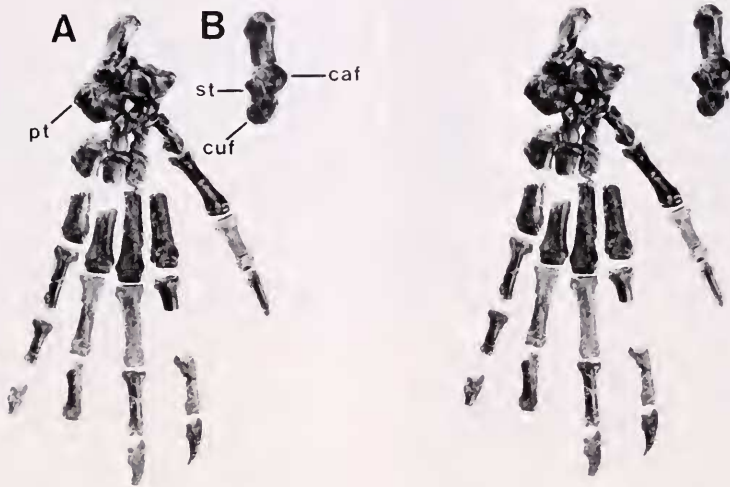


Figure 24. Stereophotographs of dorsal view of A) nearly complete right pes, and B) left calcaneum of ?*Eucosmodon* sp. (AMNH 16325). Missing from the right pes are the mesocuneiform and parts of metatarsals and phalanges of digits I–IV. Phalanges from both pedes were used to reconstruct the foot skeleton shown; their relative positions are uncertain. $\times 1.0$.

Abbreviations: *caf*, proximal calcaneoastragalar facet; *cuf*, cuboid facet; *pt*, peroneal tubercle; *st*, sustentaculum tali.

Other Material—Isolated ossicles (MCZ 20806, 20807; UA 11996) from the Bug Creek Anthills locality resemble the parafibulae of *Ptilodus kummae* in basic shape, although differences exist in the tuberosities and surface features of the blade-like muscular process. A hind limb of *Kryptobaatar dashzevegi* figured by Kielan-Jaworowska (1979: fig. 1a,c) appears to have the parafibula preserved in articulation with the fibula. The ossicle, which resembles the parafibula of *P. kummae*, contacts the fibular head near its apex; the muscular process is directed dorsally (toward the extensor surface of the femur).

PES

(Figures 4, 7, 24, 25, 26, 27; Table 1)

UA 9001—The complete right tarsus is preserved almost intact; the bones of the left tarsus are disarticulated and only the calcaneum, astragalus, cuboid, navicular, ecto- and entocuneiforms can be identified with confidence.

The robust tuber calcanei, comprising the posterior half of the bone, is laterally compressed. Its posterior terminus is dorsoventrally expanded and convex in lateral profile. The bulbous proximal facet for the astragalus (astragalocalcaneal facet) is situated just medial to the midaxial line of the tuber and becomes narrower distally (a condition differing somewhat from that in ?*Eucosmodon* sp.). A low tuberosity is developed just posterolateral to the astragalocalcaneal facet. The sustentacular facet, pyriform in outline and flat, faces medially and somewhat dorsally (approximately 50° from horizontal). The sustentacular and proximal astragalocalcaneal facets are separated by a broad sulcus. A prominent peroneal tubercle protrudes distolaterally from the calcaneal body. The cuboid facet is round, slightly concave, and faces distoventromedially.

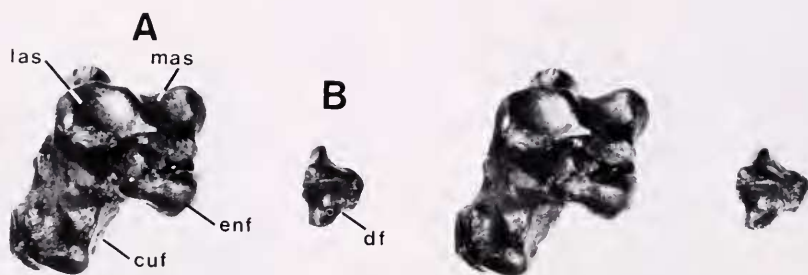


Figure 25. Stereophotographs in anterior view of A) articulated calcaneum, astragalus, and navicular, and B) entocuneiform of right pes of ?*Eucosmodon* sp. (AMNH 16325). $\times 2.3$.

Abbreviations: *cuf*, cuboid facet; *df*, distal facet for metatarsal I; *enf*, navicular facet for the entocuneiform; *las*, lateral astragalar sulcus; *mas*, medial astragalar sulcus.

The dorsal surfaces of both astragali of UA 9001 are obscured by overlying bone; other features of the astragalus appear to be very similar to those of ?*Eucosmodon* sp. (Granger and Simpson, 1929: fig. 24B), and therefore it is likely that they were similar in dorsal aspect also.

The astragalus is dorsoventrally thicker medially than laterally. The calcaneoastagalar facet, situated laterally on the plantar surface of the astragalus, is concave and anteroposteriorly elongate with a marginal indentation medially. The medial half of the plantar surface is occupied by the ventrolaterally directed sustentacular facet. The astragalar foramen pierces the posterior margin of the astragalus between the calcaneoastagalar and sustentacular facets. A canal, formed by the apposition of the calcaneal sulcus and the plantar surface of the astragalus, is a continuation of the astragalar foramen. The convex naviculoastagalar facet on the prominent astragalar head passes obliquely from the lateral border in a ventromedial and then a posteroventral direction. In perpendicular section the facet is concave and thus forms a saddle-shaped joint with the navicular.

The right pes of UA 9001 preserves the navicular in approximately articulated position. The facet for the astragalus is concave. On the distal surface are two facets; one is concave and articulated directly anteriorly with the ectocuneiform and the other appears flatter and articulated with the mesocuneiform distomedially. Contact with a dorsoventrally concave facet on the cuboid distolaterally is also present.

The rectangular cuboid has well-developed facets for the ectocuneiform medially, the navicular proximomedially, metatarsal IV distally, and metatarsal V distolaterally. The facet for the calcaneum, not wholly visible, appears to be large and shallowly concave, and extends onto the dorsal aspect of the cuboid at its proximolateral corner.

The ectocuneiform is mediolaterally compressed. Both its distal and proximal facets for metatarsal III and the navicular, respectively, are dorsoventrally concave. The ectocuneiform contacts the mesocuneiform via an oval facet. Along the proximal third of the lateral surface is an elongate facet for the cuboid.

Only the dorsal aspect of the mesocuneiform, which is rectangular in outline,



Figure 26. Stereophotographs of calcanea of North American Multituberculata. A) UA 9001, *Ptilodus kummae*, locality UAR2g, dorsal view (left); B) AMNH 77176, ?*Mesodma primaeva*, Clambank Hollow locality, dorsal view (left); C) MCZ 20782, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, medial view (left); D) MCZ 20784, ?*Stygimys kuszmauli*, Bug Creek Anthills locality, lateral view (left); E) MCZ 20783, Multituberculata indet., Bug Creek Anthills locality, ventral view (right). $\times 1.9$.

can be seen. Anteroposteriorly shorter than the ectocuneiform, it articulated with the navicular proximally, the entocuneiform medially, with metatarsal II distally (via a slightly concave facet), and with the ectocuneiform laterally.

The laterally compressed entocuneiform is the longest of the three cuneiforms. The proximal facet for the navicular is shallowly concave. The saddle-shaped distal facet for the hallux metatarsal is concave dorsoventrally and convex transversely. The ventral projection of the distal facet is narrower and more slender than the dorsal projection. Granger and Simpson (1929: fig. 23) reconstructed the pes of ?*Eucosmodon* with the narrow ventral lip of the entocuneiform in a dorsal rather than plantar position. The pes of *Ptilodus kummae* clearly shows that the narrow lip of the entocuneiform is ventral in position.

Preserved with the right tarsus of UA 9001 are two problematical ossicles. One probably articulated via a convex facet with the proximal terminus of the entocuneiform and its position indicates that it is probably a tibiale (Fig. 27A). Its other articulations are uncertain but contact with the navicular laterally, and perhaps also with the astragalus proximally, is possible. In a review of the homologies of the tibiale, Lewis (1964) pointed out that in

monotremes the tibiale articulates proximally and laterally with the astragalus and distally with the navicular. The oblique orientation of the navicular in UA 9001 provides potential space for the tibiale to have also articulated with the entocuneiform.

A second problematical ossicle is preserved in tight articulation with the distal articular surface of the fibula (Fig. 27B). Only the medial surface of the bone can be seen; it is oval in outline and quite small. It is probably not a sesamoid bone because of its position on the medial side of the distal end of the fibula. More than two tarsalia in the proximal row are unknown among mammals. Early workers (see review by Lewis, 1964) reported the occurrence of a third proximal bone (the intermedium tarsi) in pedes of several marsupials as well as in humans (the os trigonum, thought to represent the intermedium tarsi). Lewis (1964: 207) concluded, however, "that the so-called marsupial intermedium is merely a lunula within an inter-articular meniscus" and that "there is . . . little reason for regarding the anomalous human os trigonum as an intermedium tarsi. Perhaps it is not even the homologue of the marsupial lunula, and nothing more than an aberrant ossification of no morphological significance." Although the evidence is unclear, the ossicle

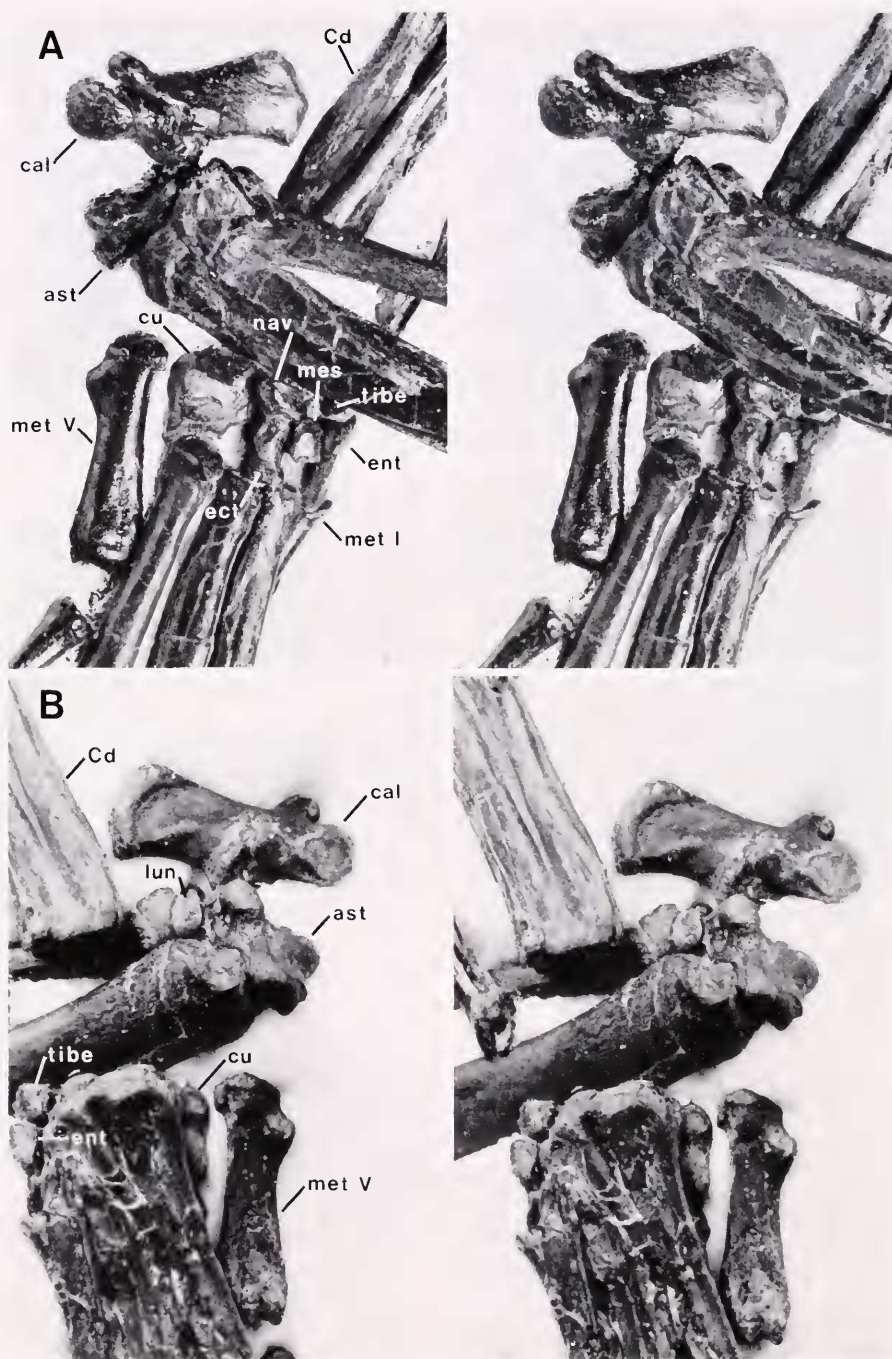


Figure 27. Stereophotographs of the right pes of *Ptilodus kummae* (UA 9001) in A) dorsal and B) ventral views. $\times 4.3$.
 Abbreviations: ast, astragalus; cal, calcaneum; Cd, caudal vertebra; cu, cuboid; ect, ectocuneiform; ent, entocuneiform; lun, lunula; mes, mesocuneiform; met I, V, first and fifth metatarsals; nav, navicular; tibe, tibiale.

TABLE 1. LIMB MEASUREMENTS (mm.) OF UA 9001 (*Ptilodus kummae*).

Digit	I	II	III	IV	V
Metatarsal length	6.9*	10.4	11.8	11.2	7.8
Proximal phalanx length	—	6.4	6.2	6.3	4.5
Middle phalanx length	—	5.7	5.7	5.5	3.8
Distal phalanx length	3.3	3.6	3.4	3.5	3.3
Length of right femur					36.4
Length of left femur					36.0
Length of right tibia					28.8
Length of right fibula					25.4
Length of right ilium (from anterior rim of acetabulum to anterior tip)					28.4

* Approximate.

associated with the distal fibula of *P. kummae* is here interpreted to be a lunula.

The relative lengths of the metatarsals are III > IV > II > V > I.

The proximal articular facet of the hallucal metatarsal is saddle-shaped (dorsoventrally convex, transversely concave). The distally directed ventral lip of the entocuneiform lies between two proximoventrally directed processes of the hallucal metatarsal, the medial one of which is larger. The shaft of metatarsal I, as in all the metatarsals, is somewhat dorsoventrally compressed. The distal articular surface cannot be seen.

Metatarsals II, III, and IV are basically similar except in length and in the shape of the proximal bases, which become progressively wider from II to IV. Metatarsal V bears a prominent, rounded lateral projection just distal to the proximal facet where a peroneal or short abductor tendon may have inserted. The proximal articular surfaces of metatarsals II to IV are dorsoventrally convex; that of metatarsal V is a flat, dorsoventrally elongate facet on the proximomedial corner of the bone.

An oblique groove between the apoposed medial side of metatarsal III and the lateral side of metatarsal II, just distal to the proximal bases, probably provided passage for a perforating metatarsal artery from the dorsal to the plantar aspect of the hind foot.

Two oval plantar sesamoids are associ-

ated with the distal ends of metatarsals IV (left pes) and V (right pes), whereas a conjoined one is present on metatarsal II (left pes).

Pedal phalanges of all ten digits are preserved. The proximal and middle phalanges of the digits are all similar except in length (Table 1), and are of a typically mammalian pattern. The proximal articular surfaces of proximal phalanges are concave. The distal articular ends of the proximal phalanges (except I) are well-rounded dorsoventrally and only slightly convex in a transverse plane; those of the middle phalanges and proximal hallucal phalanx have a prominent trochlea to accommodate the distal phalanges. The shaft of each proximal and distal phalanx tapers distally and is elliptical in cross section. Several plantar sesamoids are associated with the phalanges of both pedes.

Distal phalanges of the pes are similar in structure to those of the manus but are considerably more elongate.

Other Material—? *Eucosmodon* sp. (AMNH 16325), nearly complete right and left pedes; ? *Cimexomys minor* (UMVP 1430), left calcaneum; ? *Meniscoessus major* (AMNH 77264), left calcaneum; ? *Mesodma* sp. (UMVP 1432), right calcaneum; ? *Mesodma primaeva* (AMNH 77176), left calcaneum; ? *Stygimys kuszmauli* (UMVP 1433), right calcaneum; ? *S. kuszmauli* (MCZ 20792, MCZ 20784), left calcaneum; Multituberculata indet. (PU 14487), left calcaneum; Multituberculata indet. (MCZ 20783), right calcaneum; Multituberculata indet. (UM 72711), left astragalus.

The hind feet of ?*Eucosmodon* sp. (AMNH 16325), first described by Granger and Simpson (1929), represent the best available material for interpreting the posture and movements of a multituberculate foot. The right foot appears to lack only the mesocuneiform and various phalanges (the ectocuneiform is present, contrary to Granger and Simpson, 1929). The left foot lacks the astragalus, entocuneiform, metatarsal I, and some phalanges. It is unnecessary to recapitulate Granger and Simpson's morphological description, except to note that in their Figure 23 the entocuneiform is upside down and the hallux is depicted in a relatively adducted posture. The articular surfaces indicate that in the neutral position the hallux was divergent, probably on the order of 30° from the axis of metatarsal III.

Marsh (1889) described a calcaneum and an astragalus (YPM 10639) that he believed were from a multituberculate. Although doubts have been cast on the identity of other postcranial bones that Marsh referred at the same time to the Multituberculata (see above), McKenna (1961) agreed with Marsh's allocation of the two tarsals. Our opinion is that the calcaneum could well be that of a multituberculate, but in several features (e.g., the vestigial nature of the sustentaculum) it is unlike any other multituberculate. The astragalus is very different from that of *Ptilodus* and ?*Eucosmodon*.

OSTEOLOGY OF THE POSTCRANIAL AXIAL SKELETON

THORACIC SERIES (Figures 3, 6)

UA 9001—At least six and possibly seven posterior thoracic vertebrae are preserved in *UA 9001*; none of the anterior thoracics or cervical vertebrae were recovered. The preserved thoracic vertebrae are variously disarticulated, crushed, and fragmented.

The centra in the posterior part of the thoracic series are compressed dorsoventrally. The anterior end of each centrum is transversely elongate; the ventral half of the articular surface is recessed, and the dorsal half bulbous. The posterior articular end is almost circular in outline, except for a slight dorsal flattening, and is shallowly concave. The sides of the anterior end extend as lips to accommodate the rounded lateral margins of the preceding centrum. Below the lip, on the ventrolateral margin of the anterior end, is a costal facet for the rib head. On one of the more posterior thoracic vertebrae, a costal facet appears to have been developed on the ventrolateral margin of the posterior end, and thus the capitular articulation was intervertebral. Two shallow fossae, separated by a median crest, mark the ventral surface of each of the thoracic centra.

The pedicles are shorter than the laminae and the vertebral canal is consequently transversely elliptical. Low circular diapophyses are situated near the anterior margin of the pedicles. On the more anterior thoracics, they are protuberant and dorsally situated; on the posterior thoracics, diapophyses are developed on the pedicle-centrum junction. Stout anapophyses project caudad from the posterior margins of the pedicles.

Spinous processes in the posterior thoracic series and anterior lumbar series are triangular in cross section, the acute-angled apex of the triangle being situated along the anteroventral margin. These processes were of low enough inclination to lie between the posterodorsally directed postzygapophyses of the preceding vertebra. The precise position of the anticlinal vertebra cannot be determined. One thoracic vertebra has a spinous process which, although comminuted, appears to be in place and is more or less vertical. Two other thoracic vertebrae (assuming seven lumbar), exhibit evidence of anteriorly inclined spinous processes. The anticlinal vertebra must therefore have been located anterior to the penultimate thoracic.



Figure 28. Stereophotographs of lumbar vertebrae of ?*Eucosmodon* sp. (AMNH 16325) in A) anterior, B) right lateral, and C) dorsal (anterior is to left) views. $\times 1.0$.

The zygapophyses are robust and protuberant; the concave prezygapophyseal facets face dorsomedially, the convex postzygapophyseal facets ventrolaterally. Low ridges, one passing anteriorly from the dorsal aspect of each postzygapophysis, converge along the dorsolateral margins of the neural spine, and meet at the spine's distal terminus.

LUMBAR SERIES

(Figures 4, 5, 7, 8, 28; Table 2)

UA 9001—At least seven and possibly eight lumbar vertebrae are preserved; the last six are articulated. The thoracolumbar transition cannot be determined because of postmortem damage.

The centra of anterior lumbar vertebrae are wider than deep, as in posterior thoracics. Posteriorly the lumbar centra appear to become increasingly longer and wider, with the exception of the last lumbar, which is shorter but wider than L6 (L7?). Transverse processes extend anteroventrolaterally and become longer and broader toward the sacrum. The transverse processes of the last lumbar, however, are laterally directed.

Midventral keels are larger on anterior lumbar vertebrae than on the posterior thoracics. They appear to be absent on the posterior lumbar vertebrae. From anterior

to posterior the spinous processes of the lumbar vertebrae become more slender and more erect although an anterodorsal inclination is maintained. The zygapophyses become more robust and more widely spaced toward the sacrum.

Other Material—?*Eucosmodon* sp. (AMNH 16325), three nearly complete lumbar vertebrae; *Stygmis teilhardi* (AMNH 16024), three lumbar centra.

The spinous processes on the lumbar vertebrae of ?*Eucosmodon* sp. (AMNH 16325) (Fig. 28) are more or less vertical and, in one, the spinous process appears to be inclined slightly posteriorly (Granger and Simpson, 1929). This feature, as well as the well-developed transverse processes, indicate that the lumbar vertebrae preserved in this specimen are probably well posterior in the series. The centra are approximately circular in cross section.

SACRAL SERIES

(Figures 5, 8)

UA 9001—The first sacral vertebra is slightly shorter than the last lumbar and bears robust transverse processes that are directed laterally and slightly posteriorly. The anterior half of the terminus expands to form an articular facet for the ilium; the thin, emarginated posterior half is apparently nonarticular. The posterior end

TABLE 2. VERTEBRAL MEASUREMENTS (mm.) OF UA 9001 (*Ptilodus kummae*).

Vertebra	Length pre- to postzyga	Length centrum	Width prezyga	Width postzyga.	Width tr. processes
L1 (L2?)	7.3	—	5.4	4.4	7.1*
L2 (L3?)	8.0	—	5.7*	4.4*	8.8*
L3 (L4?)	—	—	—	4.7*	10.4*
L4 (L5?)	8.2*	—	6.1*	5.1*	—
L5 (L6?)	8.3*	—	6.2*	5.8*	13.6*
L6 (L7?)	—	—	—	—	14.9*
L7 (L8?)	—	—	—	6.2*	19.0*
S2	—	—	—	—	9.3*
Cd1	—	3.9*	—	—	8.6*
Cd2	6.2	—	5.6	4.5	—
Cd3	6.3	—	5.7	4.2	10.8*
Cd4	6.5	—	5.6	3.9*	—
Cd5	7.8	—	—	—	9.9*
Cd6	—	8.5*	—	—	9.4*
Cd7	—	10.7	—	—	8.0*
Cd8	—	11.0*	—	—	—
Cd9	—	11.2*	—	—	—
Cd10	—	11.4*	—	—	—
Cd18?	—	6.9	—	—	—
Cd19?	—	6.2	—	—	—
Cd20?	—	5.7	—	—	—
Cd21?	—	5.0	—	—	—
Cd22?	—	4.1	—	—	—
Cd23?	—	3.4	—	—	—
Cd24?	—	2.9*	—	—	—

* Approximate.

of the centrum is expanded transversely, but is not synostosed with the centrum of S2.

The second sacral vertebra is firmly synostosed with S3. The transverse processes of S2 are oriented anterolaterally. A prominent pair of ventral foramina occur on the ventral surface of the S2 centrum.

The suture between S2 and S3 is not visible. As preserved, most of S3 and its articulation with the next posterior centrum are obscured ventrally by the proximal end of the left femur. Dorsally, it appears that the centrum of S3 is fully fused with the next posterior one, indicating that the specimen has four sacral vertebrae.

At least on S3 and S4 the neural spines are prominent and erect. The centrum of S4 is elongate and relatively narrow transversely; the distal extremities of the transverse processes are missing. A large nutrient foramen occurs on the ventral

surface just posterior to the middle. Several foramina are present in the transverse processes of S4, but do not appear to be developed in other sacrals. A fragmentary haemal arch is preserved in articulation with the posteroventral margin of the centrum of S4. The distal part of the arch is broken away.

Other Material—*Stygimys teilhardi* (AMNH 16024), sacral fragment consisting of parts of two fused vertebrae (S1? and S2?).

CAUDAL SERIES

(Figures 3-8; Table 2)

UA 9001—*P. kummae* possesses at least five, and probably six, anterior caudal vertebrae (*sensu* Lessertisseur and Saban, 1967).

The transverse processes of Cd1 to Cd5

arise from almost the entire length of the centra and are directed anterolaterally (Figs. 5, 8). On succeeding caudal vertebrae transverse processes become progressively smaller and more laterally oriented. A foramen pierces the posterior base of each transverse process of the anterior caudals.

The centrum of Cd1 is only slightly longer than wide. The remaining anterior caudal vertebrae become progressively longer, the largest increase occurring from Cd4 to Cd5 (Table 2). The zygapophyses of Cd1 to Cd4 are large; on Cd5 they are small and on Cd6 the prezygapophyses are much reduced and the postzygapophyses rudimentary. The prezygapophyseal facets of the anterior caudals are saddle-shaped, that is, convex anteroposteriorly and concave transversely. As a whole, they are posteriorly inclined at a small angle to the horizontal. The spinous processes of Cd1 to Cd4 are erect, centrally located, and decrease progressively in height posteriorly such that the process of Cd5 appears to be an elongate, low, sagittal crest (it may, however, be broken).

The haemal arches ventral to the anterior caudal vertebrae are relatively large. The haemal canals are triangular, the apices being directed ventrally. The spinous processes ventral to the canals are laterally compressed, spatulate in side view, and nearly perpendicular to the centra in orientation. Further posteriorly, the spinous processes become progressively less perpendicular, projecting anteroventrally until, at about Cd10, they are nearly parallel to the centra. The haemal spine between Cd6 and Cd7 differs from those described above in being dorsoventrally rather than laterally compressed; the distal end is evenly rounded.

The proximal posterior caudal vertebrae (Cd6–Cd10) (an anterior fragment of Cd11 is also present) increase in length posteriorly, that is, the longest caudal vertebra is Cd10 or is posterior to Cd10. Cd7 to Cd10 bear anterior paired mammillary processes, transverse processes, a low, elongate spinous process, and paired an-

teroventral processes for articulation with the haemal arches. All these features decrease in size posteriorly. The centra are elongate and cylindrical, expanding slightly at their extremities. The haemal spines posterior to Cd7 are dorsoventrally compressed and bear a sagittal, U-shaped notch on the distal end, rather than being evenly rounded as on Cd6.

The positions of the three caudal vertebrae recovered by washing and screening are uncertain. However, for ease of reference, these vertebrae are tentatively identified as Cd16, Cd18, and Cd19. The processes and crests observed on Cd7 to Cd10 are only slightly developed on these caudals. In lateral view, the centra are dorsally concave and ventrally convex.

The end of the tail is preserved in UA 9001 and the individual centra are tentatively identified as Cd20 to Cd26 (Figs. 3, 6). Haemal arches on Cd20 to Cd24 are slender structures that lie parallel to and beneath the centra. Each is incised with V-shaped notches proximally and distally, the latter being the deeper.

The length of the tail can be estimated with some confidence. Twenty-one complete or partial caudal vertebrae were recovered. In view of the disparity in lengths between the articulated tenth caudal vertebra and the distal caudals (Table 2), we estimate that the tail had at least 24 and possibly as many as 28 vertebrae. The sum total of the measured and estimated lengths of the 21 known vertebrae is approximately 130 mm. Cd10 is 11.4 mm in length, and the next distal caudal preserved (Cd16?) is a disarticulated specimen that, although one end is broken, could have been no longer than 8.5 mm. Assuming a relatively large gradational length change of 1 mm, the total length of the tail would have been 150 mm with 23 vertebrae. However, gradational length changes in the two "articulated" series of posterior caudal vertebrae are less than 1 mm. It is likely, therefore, that at least three vertebrae are missing, and that minimum tail length was about 160 mm. Given the gradual increase in length in the

Cd6–Cd10 series, and assuming the unlikely of an abrupt reversal in gradient, the tail may be estimated to have been 180 mm or more in length.

Other Material—? *Eucosmodon* sp. (AMNH 16325), one anterior and four or five posterior caudal vertebrae, plus many fragments; *Styginys teilhardi* (AMNH 16024), numerous fragments of caudal centra.

Like those of *Ptilodus kummae*, the known caudal vertebrae of ?*Eucosmodon* sp. and *Styginys teilhardi* are large and robust, and indicate rather long and heavy tails.

RIBS

(Figures 3, 6)

UA 9001—Fragments of at least fifteen ribs, belonging to both left and right sides, are preserved. Several ribs are nearly complete and well preserved. On anterior ribs, the head is separated from the tubercle by a neck; the articular facet of the head is crescentic in outline, whereas the tubercular facet is larger and circular. The rib shafts are elliptical in cross section.

FUNCTIONAL ANATOMY

The postcranial skeleton of multituberculates possesses a number of unusual and even unique features. These include a scapulocoracoid with a reduced coracoid but without a suprascapular fossa, an enlarged prepollex, a dorsally emarginate acetabulum, a postobturator foramen within the ischiopubic symphysis, a large parafibula, a slender, ventrally directed lateral flange on the proximal end of the fibula, a deep excavation posteriorly beneath the proximal articular surface of the tibia, the structure of the tarsus and particularly that of the astragalus and calcaneum, and thoracic centra in which the anterior epiphysal surface is recessed ventrally and bulbous dorsally.

In this section we attempt to assess those features that may be interpreted by com-

parison with analogous conditions in other mammals. The functional significance of many features, however, remains open to speculation for lack of adequate comparative or experimental data.

SHOULDER

The scapulocoracoid of multituberculates is well advanced beyond that in morganucodontids (Jenkins and Weijs, 1979). The coracoid is reduced to a beak-like process and would not have restricted the excursion of the shoulder by virtue of a sternal articulation (as is the case in monotremes, and possibly in morganucodontids). The glenoid fossa is directed largely inferiorly as in advanced mammals. Furthermore, the glenoid appears to be relatively small.

The relative size and shape of the glenoid and humeral head are the critical features for reconstructing excursions at the glenohumeral joint. Unfortunately, an associated scapulocoracoid and humerus are unknown for any North American multituberculate, and even proximal humeri are rare (despite abundant distal humeri in collections from the Bug Creek Anthills locality). The humeral head of *Ptilodus montanus* (USNM 6076) is damaged and broken from the shaft (Fig. 11H,I) and cannot be reconstructed accurately. However, another proximal humerus that we have tentatively identified as ?*Ptilodus montanus* (USNM 9735; Fig. 11A,B,C) is basically similar to that of *Tugrigbaatar saichanensis* from the Late Cretaceous of Mongolia (Kielan-Jaworowska and Dashzeveg, 1978). The head in both is hemispheroidal and reflected dorsally. Kielan-Jaworowska and Dashzeveg (1978: 124) note that "other, undescribed multituberculate humeri from Mongolia in the (Zakład Paleobiologii) collection, belonging to the genera ?*Kryptobaatar* and *Chulsanbaatar*, show similar prominence of the head." These findings contrast to Simpson's (1928a) reconstruction of the humeral head of *Catopsalis matthewi* (AMNH 20440, also from the Late Cre-

taceous of Mongolia), which depicts a relatively flat head more or less centered on the proximal end and not reflected dorsally. However, our reexamination of the specimen reveals that the margin of the head adjoining the dorsal (extensor) surface of the shaft has been lost. Were the missing part present, the humeral head of *C. matthewi* would resemble the pattern known from other multituberculates.

Thus, on present evidence, multituberculates appear to have had considerable disparity in size between the glenoid and bulbous humeral head, indicating "... the possibility of extensive flexibility of movements of the forelimb upon the scapula" (Clemens and Kielan-Jaworowska, 1979: 117). Our assessment is that multituberculate shoulder posture and mobility were comparable to those of modern therians.

Jenkins and Weijs (1979) have suggested that the anterior surface of the large scapular spine of multituberculates may have served as the origin of a muscle equivalent to the supraspinatus. Such a reconstruction is consistent with the hypothesized mobility of the shoulder, for the supraspinatus, infraspinatus, and subscapularis are the primary muscles responsible for the integrity of the mammalian glenohumeral joint which otherwise has little structural stability.

ELBOW

Jenkins (1973) suggested that the spiral, condylar form of the multituberculate humero-ulnar joint allowed the forearm to extend in a sagittal plane as the humerus underwent rotation, adduction, and retraction during the propulsive phase. Inasmuch as similar excursions are accommodated by the spiral, trochlear humero-ulnar joint of primitive therians, the significance of the difference between the condylar and trochlear joint types is unclear. It is known that the trochlear type virtually restricts humero-ulnar movement to flexion-extension. Sloan and Van Valen (1965: 222) asserted that ulnar movements in multituberculates were

"restricted to a single plane by the shapes of the trochlea and semilunar notch" (see also Van Valen and Sloan, 1966). In order to demonstrate this, however, a detailed analysis of the joint surfaces of an *associated* humerus, ulna, and radius must be undertaken. It seems more likely that the condylar humero-ulnar joint may have provided for a second degree of freedom (rotation), a movement that Recent monotremes probably employ with a similar type of joint.

The bulbous capitulum and the sphericity of the proximal articular surface of the radius are evidence that multituberculates were capable of pronation-supination. The fact that the proximal radial facet for the ulna extends some 90° around the head indicates this capability to have been substantial.

MANUS

A sesamoid on the radial side of the wrist (usually between the scaphoid and trapezium) occurs commonly in mammals (von Bardeleben, 1894; Davis, 1964). Usually small in size (as in primates, procyonids, and ursids), the radial sesamoid is associated with various muscles (e.g., the tendon of the abductor pollicis longus in dogs; Evans and Christensen, 1979; the palmaris longus, abductor pollicis brevis and longus, and opponens pollicis of *Ailuropoda*; Davis, 1964). In certain taxa, however, the radial sesamoid is enlarged to serve specialized functions of the manus and is referred to as a prepollex. An enlarged prepollex anchors the patagium in flying squirrels (*Petaurista*), augments the fossorial capabilities of talpids (e.g., *Talpa*) and lemmings (*Lemmus*, *Dicrostonyx*), and provides additional prehension in some carnivores (e.g., *Ailuropoda*, *Potos*). The prepollex of *Ptilodus kummae* is slightly over half the length of the pollical metacarpal, and is large enough to have extended the palmar grip.

The pollex of *P. kummae*, although divergent, appears to have been limited in its movement largely to flexion-extension.

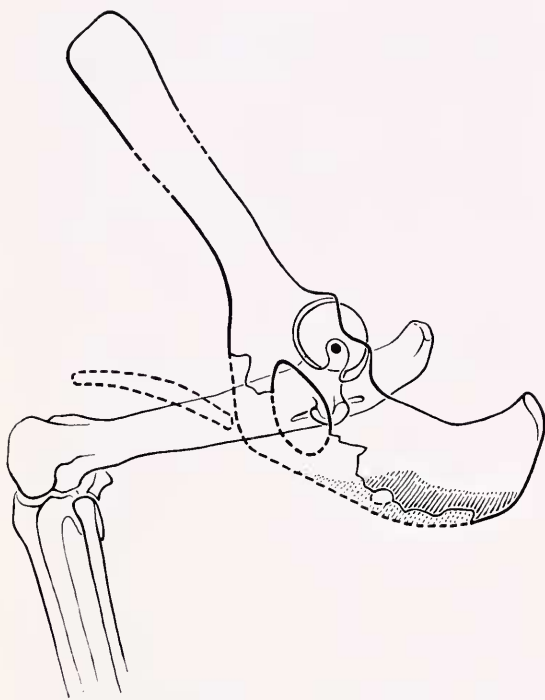


Figure 29. A reconstruction of the pelvis and hip in *?Eucosmodon* sp. (based principally on AMNH 16325) showing the relation of the fovea capitis femoris (black dot) within the acetabular fossa. The right pelvis is rendered from medial aspect and as if it were transparent. Dark cross-hatching indicates the known extent of the pelvic symphysis; light cross-hatching represents reconstructed symphyseal area. Note that the dorsal margin of a postobturator foramen is present. $\times 1.1$.

The pollical carpo-metacarpal joint is not saddle-shaped. The proximal surface of metacarpal I is broad and articulated with flat facets on the distal surfaces of the trapezium and trapezoid and the proximo-medial surface of metacarpal II.

PELVIS AND HIP

Van Valen and Sloan (1966: 276) cited a "dorsally open" acetabulum among the several postcranial features of multituberculates that they hypothesized to be inferior to the therian condition. They concluded that the femur must have been "held in articulation only by muscles in this direction. This suggests a near or com-

plete lack of ricochet or gliding habits among multituberculates and may have permitted at most only a low possibility of arboreal activity." Our assessment of this feature is different. A number of the-rian joints, most notably the glenohumeral, rely largely on muscles for stabilization; those that function in this manner are typically highly mobile. It is possible, therefore, that the absence of bone around the dorsal aspect of the multituberculate acetabulum provided for an unusual degree of femoral mobility, particularly in abduction. Elftman (1929) noted that in certain arboreal marsupials, most notably in the gliding phalanger *Petauroides*, the dorsal margin of the acetabulum is incised to facilitate femoral abduction. We think it likely that at least part of the dorsal "hiatus" of multituberculates was closed by fibrocartilaginous tissue such as typically occurs in mammals (the acetabular labrum) and bridged the acetabular notch as the transverse ligament. Thus reconstructed, multituberculates possessed a relatively shallow acetabulum, indicative of highly mobile hind limbs (see Jenkins and Camazine, 1977).

The position of the fovea capitis femoris on the femoral head indicates that multituberculates employed an abducted femoral posture. The fovea represents the point of attachment of the ligamentum capitis femoris which is confined within the acetabular fossa; displacements of the fovea observed in various mammals are related to differences in femoral posture and excursion (Jenkins and Camazine, 1977). In multituberculates, the fovea is located on the ventral (flexor) side of the head. Assuming that the acetabulum and acetabular fossa are aligned more or less in a sagittal plane, such a location of the fovea requires that the femur be considerably abducted (Fig. 29). In a neutral posture the long axis of the femur is estimated by this method to lie at about 45° to the median plane.

The postobturator foramen, unknown in any other order of mammals, is open

to speculation in terms of its function. The lateral surface of the ischium in mammals is typically the site of origin of muscles that adduct or externally rotate the femur. The postobturator foramen is located within the symphysis along the ventral margin of the ischium; it does not communicate with the pelvic cavity. In this region it is logical to reconstruct the attachment of femoral adductors. In comparison with the pelvis of other mammals, the multituberculate ischium presents an unusually broad area for muscle attachment. It is possible that the stress of opposing adductors along the ventral margin of the ischium is responsible for the fenestration. A functionally analogous situation may be with the true obturator foramen where the obturator externus and internus act from opposite sides of a common membrane.

Kielan-Jaworowska (1979) analyzed the possible relationship between pelvic structure and reproduction in a Cretaceous multituberculate (*Kryptobaatar dashzevegi*) from Mongolia. Noting the overall relative narrowness of the pelvis, the acute angle of intersection between the two sides, and the extensive fusion along the keel-like ischiopubic symphysis, she calculated the dimensions of the pelvic outlet which led her to the conclusion that multituberculates were viviparous and had extremely small neonates.

KNEE

Femoral condyles of multituberculates are confined to the inferior (flexor) aspect of the bone, and do not extend around the distal extremity to be contiguous with the patellar groove. From this evidence, multituberculates employed the crouched posture characteristic of primitive mammals and appear to have been incapable of extending the knee much beyond 120°. The orientation of the center of the femoral condyles indicates that the tibia, in the middle of its range of excursion, articulated with the femur at about 90°.

The asymmetry of the femoral condyles and the eccentricity of the patellar groove in multituberculates is similar to that in morganucodontids and certain primitive therians (Jenkins and Parrington, 1976). The possibility that joints of this type are adapted to accommodate some rotation at the knee during the propulsive phase remains to be investigated.

The parafibulae of *Ptilodus kummae* are relatively large. Parafibulae are found in various marsupials and rarely in eutherians; in monotremes they occur as prominent, broad flanges synostosed to the proximal end of the fibulae and in *Ornithorhynchus*, at least, provide attachment for the long digital flexor, long peroneal, soleus, plantaris, and peroneal flexor muscles (Lessertisseur and Saban, 1967). In size and shape the parafibulae of *P. kummae* resemble more closely those of monotremes than the ill-defined ossicles found in therians. Unlike the monotreme conditions, however, they articulate with the fibula via a synovial joint. The possible homologies of the parafibulae, as well as the functional implications of their presence or absence, are not well understood (for a discussion, see Lessertisseur and Saban, 1967).

PES

The tibio-astragalar and astragalocalcaneal joint surfaces in all the multituberculate specimens available for this study exhibit the same basic features, and are indicative of an unusual range of pedal movements that are typically employed by mammals that climb.

The tibio-astragalar joint not only appears to have allowed dorsiflexion and plantarflexion, but abduction and eversion as well. The dorsal (proximal) surface of the astragalus bears two subparallel sulci, one medial and the other lateral (Fig. 25). The sulci are approximately aligned with the hallux (Fig. 24A) and received the medial and lateral condyles on the distal end of the tibia (Figs. 22, 30A₂). Some

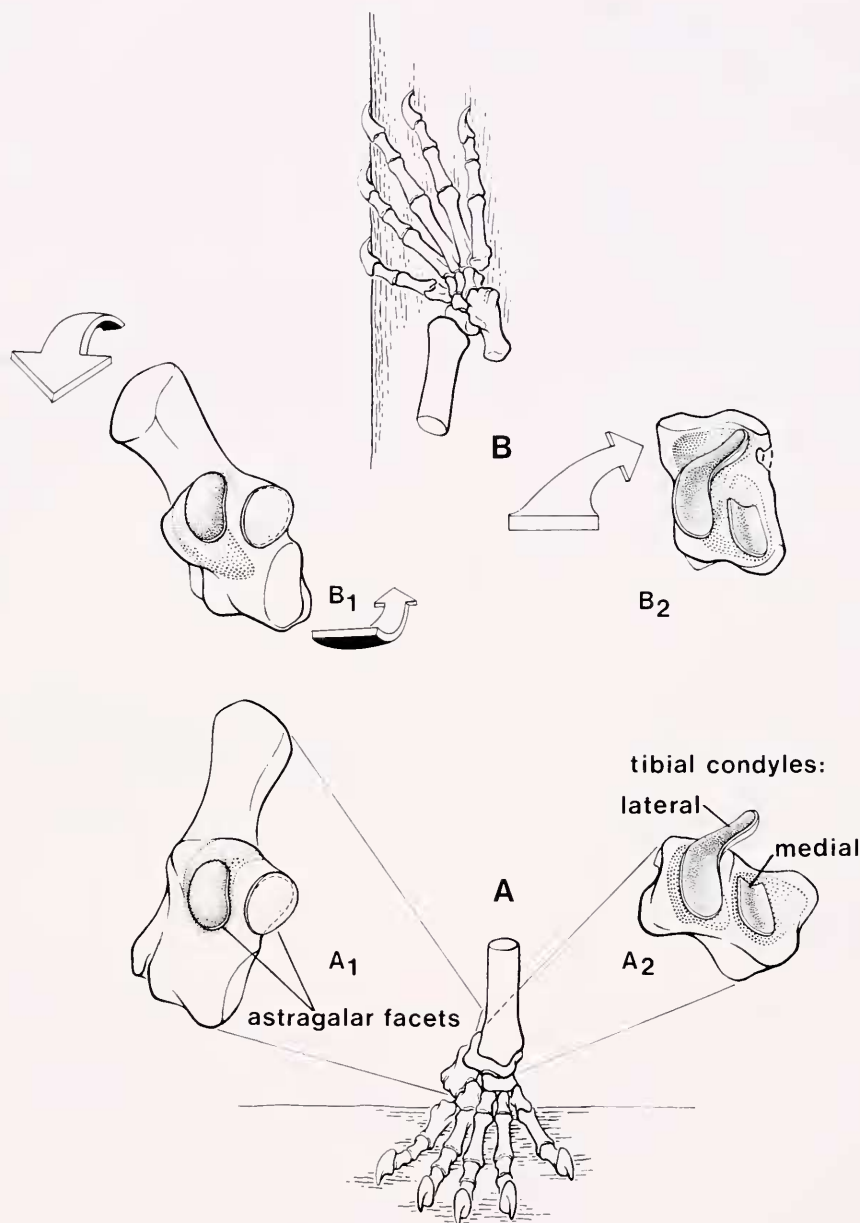


Figure 30. Tarsal movements in a multituberculate foot, interpreted from the pedes of ?*Eucosmodon* sp. (AMNH 16325) and *Ptilodus kummae* (UA 9001), that position the foot to secure a grip during headfirst descent. (A) the neutral position: the relations of the astragalar facets to the calcaneum (**A₁**) and the relations of the tibial condyles to the astragalar sulci (**A₂**) are shown. (B) The reoriented position: rotation at the astragalocalcaneal joint (**B₁**) yields plantarflexion and inversion. Rotation at the tibio-astragalar joint (**B₂**) yields abduction and eversion. Additional adjustments permitting inversion-eversion and dorsiflexion-plantarflexion are possible at the astragalonavicular and calcaneocuboid joints. The reoriented position of the foot also requires extension at the hip joint, thus repositioning the tibia and fibula nearly parallel to the substrate in (B), in contrast to the nearly perpendicular orientation in (A). The fibula is not shown.

plantarflexion and dorsiflexion could have been effected by the astragalar sulci rocking backwards and forwards across the most distal surfaces of the tibial condyles. Additional plantarflexion and dorsiflexion were possible at the astragalocalcaneal joints (Figs. 30A₁, B₁).

Abduction and related movements suitable for securing grips over a wide range of foot postures appear to have been accommodated by the asymmetrical configuration of the tibial condyles. The lateral condyle is longer than the medial, and wraps spirally around the distal end of the tibia from its anteromedian to posteromedian margins (Fig. 22). The short, linear medial condyle extends from the anterior margin to the center of the distal end; it is oriented anteromedially-posterolaterally. From the neutral position (Fig. 30A₂), translation of the astragalar sulci along the tibial condyles of different length resulted in abduction of the hind foot. In this movement, the lateral sulcus translated along the semilunar lateral tibial condyle, whereas the medial sulcus rolled and pivoted about the medial condyle (Fig. 30B₂). The lateral condyle, furthermore, is spiral; the anterior part of the articular surface faces distally, the posterior part (extending onto the posterior surface of the tibia) posteromedially. This spiral shape caused the astragalus to evert (i.e., the volar surface of the foot turned outward) as it was abducted.

In addition to the excursion at the tibioastragalar joint, the foot had to be plantarflexed in order to secure a grip for headfirst descent (Fig. 30B). This movement occurred at the astragalocalcaneal joint (Figs. 30A₁, B₁) and involved pivoting the calcaneum about an axis through the sustentaculum tali; the facet of the sustentaculum and its counterpart on the astragalus are nearly equal in size, and thus give no evidence of substantial translatory movement. Excursion at the proximal calcaneoastragalar joint, however, did involve translation. The bulbous proximal calcaneoastragalar facet provided a semi-

lunar pathway, and full plantarflexion involved a degree of conjunct inversion (Fig. 30B₁).

Additional postural adjustments of the foot for climbing on uneven substrates could have been accommodated at the calcaneocuboid and astragalonavicular joints. The cuboid facet on the calcaneum is slightly concave and is larger than the reciprocally convex facet on the cuboid (Fig. 24). The long axis of the saddle-shaped astragalonavicular joint is oriented dorsolaterally-ventromedially (Fig. 25). Translation of the navicular along this axis would have contributed to inversion-eversion, whereas movements normal to the long axis would have provided additional dorsiflexion-plantarflexion. Conjunct movements at the calcaneocuboid joint appear to have been possible for each of these actions.

The amount of abduction permitted by the tibioastragalar joint was on the order of 90°. Consistent with the degree of femoral abduction reconstructed on the basis of hip structure (see above), the normal stance of the foot probably also involved an abducted posture. Our estimate is that the longitudinal axis of the foot (passing along the third metatarsal) deviated 30° to 40° from a sagittal plane. With an additional 90° of abduction possible at the tibioastragalar joint, the foot could have readily assumed the posture depicted in Figs. 30 and 31. This posture involved repositioning the tibia and fibula nearly parallel to the vertical substrate, in contrast to the more or less perpendicular orientation in a stance on a horizontal substrate. Such a movement could have been accomplished through hip extension (the femoral condyles of multituberculates indicate that knee extension was limited).

The distal facet on the entocuneiform is saddle-shaped (concave dorsoventrally, convex mediolaterally) and permitted both flexion-extension and abduction-adduction of the hallux. However, the convexity is asymmetrical; the facet extends farther medially than it does laterally, a feature

that is directly indicative of an unusual degree of hallucal abduction.

A divergent, abductable hallux is typical of small mammals that move on uneven surfaces. Mammals that descend vertical surfaces (such as tree trunks) headfirst are capable of reorienting the hind foot, thus pointing the toes backward and positioning the claws to secure a grip. The presence of features in the hind foot of multituberculates that would permit the same kind of behavior may be taken as one line of evidence that some multituberculates, at least, were arboreal in habit.

The characters of the terminal phalanges of both manus and pes indicate well-developed falculae *sensu* Le Gros Clark (1936). Extensive trochleae at the distal interphalangeal joints and protuberant flexor tubercles and extensor processes are evidence of claws capable of strong, gripping action.

TRUNK

The partial skeleton of *Ptilodus kummae* (UA 9001) provides an opportunity for reconstructing limb and body proportions (Fig. 31). The fact that the anterior thoracic and the entire cervical series is missing in this specimen requires some extrapolation. The following is an account of how the length of the pre-caudal vertebral column was determined.

The sacral and lumbar regions are completely represented, although some of the vertebrae are crushed or otherwise distorted. The combined length of the four sacral vertebrae is ca. 24.5 mm. The lumbar series comprises at least seven vertebrae, and possibly eight. If seven lumbar vertebrae are assumed, the total length of the lumbar series measured along the ventral aspect is 46.5. If the lumbar series is measured from its dorsal aspect, the total

length is 44.1. The lumbar series may therefore be safely estimated to be between 40 and 50 mm in length.

Only a few of the posterior thoracic vertebrae are sufficiently well preserved to permit mensuration. Of these, three have centra, 4.0, 4.25, and 4.5 mm in length. On this basis, if it is assumed that the length of thoracic vertebrae decreases anteriorly (as in most mammals) and that the average length of the vertebrae is 4.25 mm, then the total maximum length of the thoracic column is about 51 mm for twelve vertebrae and 55 mm for thirteen. The thoracic series was therefore probably between 45 and 55 mm in length.

In the absence of all cervical vertebrae in this specimen, the length of the neck had to be estimated from the relative proportions known in other mammals. For *Tupaia glis*, *Didelphis marsupialis*, and *Procyon lotor*, the cervical vertebral column ranges from 16 to 22 percent of the total length of the sacral, lumbar, and thoracic series. Using 19 percent as an average, the estimated cervical series length in *P. kummae* would be between ca. 22 and ca. 24.5 mm depending on whether trunk length was as little as ca. 110 or as much as ca. 130 mm.

When these variables are taken into consideration, trunk length estimates range from about 130 to 155 mm for *P. kummae*. In Figure 31 the total length of the precaudal vertebral column is depicted to be 138 mm.

TAIL

The tail in mammals may serve a variety of functions: behavioral, protective, thermoregulatory, postural, and locomotor. Among the orders Marsupialia, Rodentia, Edentata, Pholidota, Carnivora, and Primates, some taxa have evolved both

Figure 31. Reconstruction of a multituberculate skeleton based principally on a specimen of *Ptilodus kummae* (UA 9001). The body is positioned in headfirst descent. In this posture the thoracolumbar region is extended, the hind foot is reoriented such that the toes point backward, and the tail is employed as a grasping and stabilizing organ.



musculoskeletal and neural specializations to effect prehensility, that is, the tail is sufficiently robust, and its movements so precisely controlled, as to serve as a "fifth limb." Well-known examples are various species of the genera *Caluromys*, *Didelphis*, *Marmosa*, *Philander*, *Phalanger*, *Pseudocheirus*, and *Trichosurus* among marsupials; *Capromys prehensilis*, *Coendou* spp., and *Pithecheir melanurus* among rodents; *Tamandua tetradactyla* and *Cyclopes didactylus* among edentates; *Manis tricuspis* among pholidotans; *Arctictis binturong* and *Potos flavus* among carnivores; and species of the genera *Cebus*, *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix* among primates. All of these taxa employ the prehensile tail in climbing; all may be considered arboreally adapted despite variations in allocation of time spent on the ground or in trees.

A preliminary survey of prehensile-tailed mammals reveals a number of shared features in their caudal structure. The tail is long, commonly twice or more the length of the precaudal vertebral column; in a few taxa the tail is shorter (e.g., in *Didelphis*, where the tail is 1.2 times the length of the precaudal vertebral column). Haemal arches are developed along nearly the entire length of the tail. Transverse processes are robust, and are present even on the most distal caudals. Finally, the sacral spinous processes are relatively large, commonly nearly equalling in height the spinous processes of posterior lumbar vertebrae. The last three features appear to be related to the hypertrophy of the caudal musculoskeletal system necessary for increased gripping strength.

The tail of *Ptilodus kummae* gives evidence of most of these bony features. The tail, estimated at 180 mm, is 1.2 to 1.4 times the length of the precaudal vertebral column. Transverse processes are well developed, even on the distal caudals. Haemal processes are large, and present along the entire length of the tail. The sacral spinous processes, to the extent that their height can be estimated, appear to

have been as prominent as those on the posterior lumbar vertebrae. From this evidence, *P. kummae* possessed structural adaptations that, in living mammals, are related to tail prehensility and arboreal habits.

DISCUSSION AND CONCLUSIONS

The present review provides evidence of substantial homogeneity in postcranial structure among North American multituberculates of the suborders Ptilodontidea and Taeniolabidoidea. Despite the diversity of multituberculates, both in size and in dental specializations, postcranial bones exhibit little variability in proportions or in features distinctive of the order. Our assessment is based on those parts of the skeleton for which there is adequate representation: basal scapulocoracoid, distal humerus, proximal ulna, pelvis, femur, proximal tibia, and calcaneum. Where slight differences are apparent (for example, compare the anterior tip of the ilium in *Ptilodus*, Fig. 8, with that of ?*Eucosmodon*, Fig. 18), they do not appear to be of major functional significance. Confidence in our conclusion that North American multituberculates exhibited little postcranial diversification must be tempered by the realization that most material available at present is disarticulated and dissociated. It is possible that the future recovery of associated skeletons will reveal a modest array of taxon-specific adaptations, especially in proportions. However, in the one comparison (metatarsal III/femur length) permitted by the specimens of *Ptilodus kummae* (UA 9001) and ?*Eucosmodon* sp. (AMNH 16325), there is only a negligible difference ($P. = .31$, $E. = .29$) despite the fact that ?*Eucosmodon* is almost twice as large as *Ptilodus* and is not closely related.

Several workers have speculated on the locomotor habits of multituberculates. Gidley (1909: 621) believed that the "relatively large proportions of the pelvis and

hind limbs strongly suggest that *Ptilodus* was saltatorial . . ." Simpson (1926: 247) alluded to the limb proportions of Recent mammals in reaching his conclusion that *Ptilodus* ". . . was probably a swiftly moving and agile quadruped, and that there is nothing in the known proportions of the limbs which indicate in any certain way a terrestrial or an arboreal habitat." Nonetheless, Simpson (1926: 249) concluded from the herbivorous dentition of multituberculates (and the abundant evidence of trees) that "it would be remarkable if many [multituberculates] were not at least semi-arboreal." In a study of the hind limb of ?*Eucosmodon*, Simpson and Elftman (1928: 15–16) observed that the hind foot had ". . . great flexibility, grasping power with opposable hallux, and . . . sharp claws. Neither in its proportions nor morphological features does this hind foot show fossorial or saltatory adaptations. This and other known characters definitely suggest a quadrupedal animal, well adapted for possible arboreal life but also capable of rapid progression on the ground."

The conclusion from the present study is that some multituberculates, at least, were arboreal in habit (Fig. 31). The primary evidence is derived from the hind foot and tail. In both *Ptilodus* and ?*Eucosmodon* the tibio-astragalar and other tarsal joints are specialized for a range of pedal mobility (especially abduction, permitting headfirst descent) characteristic of arboreal mammals. The hallux was divergent, and the entocuneiform-metatarsal I joint permitted considerable abduction and adduction for prehension in a plane independent of the remaining digits. The long, robust tail of *Ptilodus* possessed musculoskeletal features that, in modern mammals, are present in prehensile-tailed forms. Several other features tend to corroborate this interpretation, although by themselves they are secondary and not definitive evidence: the apparent mobility of the scapulocoracoid and the glenohumeral and hip joints, the large prepollex in *Ptilodus* (possibly augmenting the grasp), and

narrow, elongate ungual phalanges with well-developed flexor tubercles and extensor processes (indicating sharp, powerful claws).

Our interpretation of several features in *Ptilodus kummae* as adaptations for climbing does not imply that this or other multituberculate taxa were exclusively arboreal. Jenkins (1974) pointed out that arboreal and terrestrial activity requires basically the same locomotor repertoire of small sized mammals that must climb and grip and span discontinuous substrates in both settings. In the case of tree shrews, for example, species may be either "arboreal" or "terrestrial" (or both) in the sense of habitat preference although such a distinction is not evident in musculoskeletal differences. Several tree shrew adaptations (notably the excursions possible in the thoracolumbar region, the shoulder and hip joints, the tarsus and the hallux) are employed in moving and climbing on disordered substrates whether on the forest floor or in trees. Inasmuch as multituberculates appear to have possessed comparable locomotor adaptations, their habitats could have been at least as diverse.

However, two aspects of the postcranial skeleton of *P. kummae*, the structure of the tarsus and tail, represent unusual specializations that in living mammals are used primarily in arboreal locomotion. Furthermore, although evidence for a prehensile tail is available only for *P. kummae*, evidence for tarsal adaptations that permit headfirst descent is known in multituberculate taxa of different body sizes (?*Mesodma* sp., *Ptilodus kummae*, *Stygimys teilhardi*, and ?*Eucosmodon* sp.). *Mesodma*, *Ptilodus*, and *Stygimys* are roughly comparable to tupaiids in size, but *Eucosmodon* is comparable to *Didelphis* and clearly larger than the small mammal size class referred to by Jenkins (1974). Thus, based on present evidence, North American multituberculates over a range of sizes appear to have employed specialized foot postures; because of this, we in-

interpret their specialized tarsal structure as an arboreal adaptation rather than as a response to the locomotor requirements of small mammals.

Multituberculates were a major component of early mammalian faunas, persisting with their characteristic specializations from at least the Late Jurassic to the Oligocene. The possible factors contributing to their extinction have been considered by several workers. Van Valen and Sloan (1966: 277) documented the decrease in multituberculate abundance that took place after a peak in the Late Cretaceous, although they determined that maximal taxonomic diversity occurred during the middle Paleocene. These authors suggested that "the decline of the multituberculates was probably initiated by competition with condylarths, increased by primates, and completed by rodents." Hopson (1967: 354) emphasized that multituberculates were "at best 'submetatherian' in evolutionary grade," but recognized, as did Van Valen and Sloan, that primitive structural features do not necessarily entail competitive disadvantages. Nonetheless, Hopson thought it plausible to suggest an "explanation for the competitive inferiority of the multituberculates to placental herbivores in the early Tertiary: the Cretaceous and earliest Paleocene multituberculates remained significantly below the eutherian level of advancement in nearly all areas of their biology, and their continued survival, and even diversification, depended principally on the fact that they were still the only mammalian occupants of the herbivorous adaptive zone." However attractive is Hopson's hypothesis, our review of the postcranial skeleton of North American forms provides no evidence of features that might be considered significantly inferior to those of eutherians. Skeletal traits that are clearly divergent in multituberculates and eutherians cannot be assessed in terms of comparative locomotor ability, particularly because many such multituberculate features have no analogs among living mammals. The factors contributing to

multituberculate extinction, including the possibility of competitive inferiority, must always remain inferential. Yet it is possible to analyze, in terms of function, many skeletal structures in extinct mammals. Such analyses as we have attempted here have been facilitated by other studies, both anatomical and experimental, that have elucidated specific aspects of mammalian postcranial biomechanics. We believe that further advances in our knowledge of multituberculates will depend as much on neontological as on paleontological investigations.

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